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A ‘little dragon’ from Kunming City: a new green pit viper from Yunnan Province, China (Squamata, Viperidae, *Trimeresurus*)

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Abstract

A new species of the genus *Trimeresurus* Lacépède is described from Kunming City, Yunnan Province, China, based on an integrative analysis of morphological and molecular data. The new species, *Trimeresurus loong* **sp. nov.**, is assigned to the subgenus *Viridovipera* Malhotra & Thorpe and can be distinguished from its congeners by the following combination of characters: the first supralabial completely separated from the nasal scale; a short and spinose hemipenis; moderate adult body size; dorsal scales in 19 (21 or 23)-19-15 rows; 150–151 ventral scales in males, and 157–158 in females; 67–68 subcaudals in males, and 57–64 in females; and distinct body color patterns. Molecular analyses based on the mitochondrial *16S*, cyt *b*, and *ND4* gene fragments indicate that *Trimeresurus loong* **sp. nov.** is genetically divergent from all currently recognized congeners, showing uncorrected *p*-distances ranging from 6.7–11.2% in cyt *b* and 6.1–8.3% in *ND4*. The discovery of this species brings the total number of recognized *Trimeresurus* species to 57, including nine recorded from Yunnan Province, further emphasizing the complex topography and exceptional level of endemism.

Key Words

Hemipenis, molecular phylogeny, morphology, taxonomy, *Trimeresurus loong* sp. nov., Southwestern China, systematics

Introduction

The genus *Trimeresurus* Lacépède, commonly known as Asian green pit vipers, represents one of the most species-rich and taxonomically challenging groups within the subfamily Crotalinae Oppel. These venomous snakes are of considerable medical importance and are widely distributed across tropical and subtropical Asia, from the Himalayas and southern China to mainland and insular Southeast Asia, extending as far as Timor and the Lesser Sunda Islands (Gumprecht et al. 2004; Malhotra and Thorpe 2004a; David et al. 2011, 2023; Poyarkov et al. 2023; Mirza et al. 2023). Species of *Trimeresurus* exhibit remarkable ecological and morphological diversity,

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which, together with sexual dimorphism and geographic variation, have long complicated their taxonomy. Extensive revisions during the past two decades have resulted in the recognition of multiple lineages and numerous new species, particularly from Indochina and southern China (Vogel et al. 2023; Idiiatullina et al. 2023, 2024a–c; Pawangkhanant et al. 2025; Xu et al. 2025). At present, 57 valid species are recognized in the genus (Mirza et al. 2023; Idiiatullina et al. 2023, 2024a–c; Pawangkhanant et al. 2025; Uetz et al. 2025). Despite numerous taxonomic revisions in recent years, species diversity within *Trimeresurus* remains incompletely resolved. High morphological similarity among species, coupled with pronounced sexual dimorphism and geographic variation, often obscures diagnostic differences and conceals cryptic lineages (e.g., Malhotra and Thorpe 2004a,b; Rathee et al. 2022; Nguyen et al. 2024; Idiiatullina et al. 2023, 2024a–c; Liang et al. 2025; Xu et al. 2025).

According to the classification proposed by Mirza et al. (2023), *Trimeresurus* is currently divided into six subgenera: *Trimeresurus* sensu stricto, *Parias* Gray, *Popeia* Malhotra & Thorpe, *Himalayophis* Malhotra & Thorpe, *Sinovipera* Guo & Wang, and *Viridovipera* Malhotra & Thorpe (see also Idiiatullina et al. 2024b; Pawangkhanant et al. 2025; Xu et al. 2025). Members of *Viridovipera* are defined by two key morphological features: the first supralabial scale is completely separated from the nasal scale, and the hemipenis is short and spinose (Malhotra and Thorpe 2004a; Dawson et al. 2008; Mirza et al. 2023). Currently, eight species are assigned to this subgenus, including *T. mayaae* Rathee, Purkayastha, Lalremsanga, Dalal, Biakzuala, Muansanga & Mirza [type locality: Champhai District, Mizoram State, India], *T. medoensis* Zhao [type locality: Motuo (Medog) County, Xizang Autonomous Region, China], *T. nujiang* Liang, Ding, Vogel, Chen & Wu [type locality: Cikai Town, Gongshan County, Nujiang Lisu Autonomous Prefecture, Yunnan Province, China], *T. pretiosus* Xu, Nguyen, Wang, Zhang, Poyarkov, Wei, Vogel, Peng & Weng *in* Xu, Nguyen, Wang, Zhang, Poyarkov, Wei, Vogel, Li, Deng, Sun, Peng & Weng [type locality: Xiayadong Township, Yadong County, Xigaze City, Xizang Autonomous Region, China], *T. stejnegeri* Schmidt [type locality: Shaowu City, Nanping Prefecture, Fujian Province, China], *T. truongsonensis* Orlov, Ryabov, Bui & Ho [type locality: Phong Nha-Ke Bang National Park, Quang Binh Province (now Quang Tri Province), Vietnam], *T. vogeli* David, Vidal & Pauwels [type locality: Khao Yai National Park, Nakhon Ratchasima Province, Thailand], and *T. yunnanensis* Schmidt [type locality: Tengchong City, Baoshan City, Yunnan Province, China] (see Rathee et al. 2022; Liang et al. 2025; Xu et al. 2025).

Yunnan Province, situated at the junction between the Palearctic and Oriental Realms, is recognized as one of China's major biodiversity hotspots. It harbors a particularly rich pit viper fauna, including several narrowly distributed *Trimeresurus* species. Currently, eight species of *Trimeresurus* are recorded from Yunnan Province: three of the subgenus *Trimeresurus* (*T. albolabris* Gray, *T. guoi* Chen, Shi, Vogel & Ding *in* Chen, Shi, Gao, Vogel, Song, Ding & Dai, and *T. caudornatus* Chen, Ding, Vogel & Shi *in* Chen, Yu, Vogel, Shi, Song, Tang, Yang, Ding & Chen); two of *Popeia* (*T. popeiorum* Smith and *T. lanna* Idiiatullina, Nguyen, Pawangkhanant, Suwannapoom, Chanhome, Mirza, David, Vogel & Poyarkov); and three of *Viridovipera* (*T. stejnegeri* Schmidt, *T. yunnanensis* Schmidt, and *T. nujiang* Liang, Ding, Vogel, Chen & Wu) (e.g., Idiiatullina et al. 2024b; Nguyen et al. 2024; Liang et al. 2025). Although Yunnan has been the focus of numerous herpetological studies, recent surveys have revealed that many montane valleys and forested gorges in southwestern China remain insufficiently explored. During fieldwork conducted in 2025 in Qinglong Town, Anning City, Kunming City, Yunnan Province, China, we discovered a population of green pit vipers that could not be assigned to any known species. Morphological examination and mitochondrial DNA analyses (*16S*, cyt *b*, and *ND4* genes) confirmed that this population represents an undescribed species of *Trimeresurus*. We therefore describe it herein as a new species.

Material and methods

Sampling and specimen preservation

Fieldwork was conducted in forested areas of Anning City, Kuming City, Yunnan Province, China in May and September 2025 (Fig. 1). Geographic coordinates and elevation were recorded using the TwoStep Outdoor Assistant v7.9.13 (Shenzhen 2bulu Information Technology Co., Ltd., China). Specimens were located using snake hooks, photographed in life, and humanely euthanized with a buffered MS-222 (tricaine methanesulfonate) solution. Subsequently, specimens were fixed in 10% formalin and transferred to 75% ethanol for long-term preservation. Liver tissue samples were collected fresh, preserved in 95% ethanol, and stored at –20 °C for molecular analyses. All voucher specimens were deposited in the herpetological collection of Qinghai University, Qinghai Province, China (QHU). All procedures followed the regulations of the Wildlife Protection Law of China and were approved by the Institutional Ethics Committee of Qinghai University (Protocol No. PJ202501-89).

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from ethanol-preserved liver tissues using the QIAamp DNA Mini Kit (QIAGEN, Changsheng Biotechnology Co. Ltd., Changchun, China). Three mitochondrial DNA (mtDNA) fragments, including 16S ribosomal RNA (*16S*), cytochrome *b* (cyt *b*), and NADH dehydrogenase subunit 4 (*ND4*), were am-

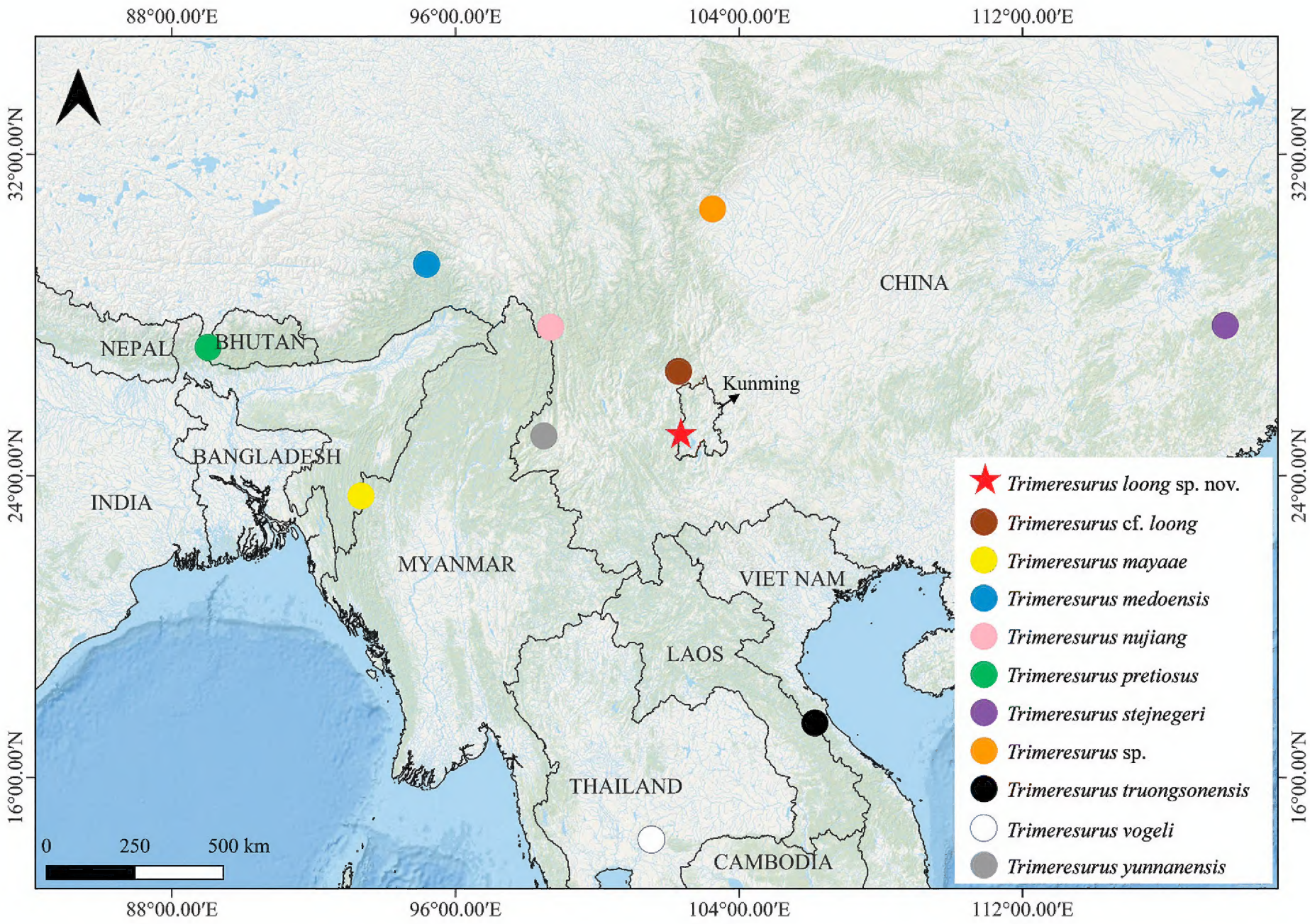

Figure 1. Map showing the type localities of the new species and other *Trimeresurus* species of the subgenus *Viridovipera*. **Red star:** *Trimeresurus loong* sp. nov. from Anning, Kunming, Yunnan, China; **brown circle:** *T.* cf. *loong* from Huili, Sichuan, China; **yellow circle:** *T. mayaae* from Champhai, Mizoram, India; **blue circle:** *T. medoensis* from Motuo (Medog), Xizang, China; **pink circle:** *T. nujiang* from Gongshan, Yunnan, China; **green circle:** *T. pretiosus* from Xiayadong, Yadong, Xizang, China; **purple circle:** *T. stejnegeri* from Shaowu, Fujian, China; **orange circle:** *Trimeresurus* sp. from Chengdu, Sichuan, China; **black circle:** *T. truongsonensis* from Phong Nha-Ke Bang NP, Quang Tri, Vietnam; **white circle:** *T. vogeli* from Khao Yai NP, Nakhon Ratchasima, Thailand; and **grey circle:** *T. yunnanensis* from Tengchong, Yunnan, China.

plified using polymerase chain reaction (PCR). The amplification of *16S* was conducted with primers 16S1LM (5′-CCGACTGTTGACCAAAAACAT-3′) and 16SH1 (5′-TCCGGTCTGAACTCAGATCACGTAGG-3′), following the protocol of Nguyen et al. (2020). For cyt *b*, we used primers L14910 (5′-GACCTGTGATMTGAAAACCAYCGTTGT-3′) and H16064 (5′-CTTTGGTTTACAAGAACAATGCTTTA-3′), as described by Burbrink et al. (2000). The *ND4* fragment was amplified using Trim-ND4F (5′-CACCTATGACTACCAAAAGCTCATGTAGAGC-3′) and Trim-ND4LEUR (5′-CATTACTTTTACTTGGATTTGCACCA-3′), following Salvi et al. (2013). The PCR thermal cycling profile was as follows: initial denaturation at 95 °C for 3 min; followed by 36 cycles of denaturation at 95 °C for 30 s, annealing at 48 °C for 45 s, and extension at 72 °C for 1 min; with a final extension at 72 °C for 10 min; and a final hold at 4 °C. PCR products were sequenced by Shanghai Map Biotech Co., Ltd. (Shanghai, China). Raw sequences were assembled using SeqMan (DNASTAR; Burland 2000), and newly generated sequences were submitted to DDBJ (Table 1).

Phylogenetic analysis

For phylogenetic analysis, a total of 235 sequences were included (Table 1), of which 21 were newly generated in this study, while 214 were retrieved from two public databases: GenBank and GenBase (National Genomics Data Center (NGDC), Beijing Institute of Genomics, Chinese Academy of Sciences / China National Center for Bioinformation; Bu et al. 2024; CNCB-NGDC Members and Partners 2025). These included representatives from 34 species of *Trimeresurus* and two outgroup taxa: *Craspedocephalus puniceus* (Boie) and *Peltopelor malabaricus* (Jerdon). Sequences were aligned in MEGA X (Kumar et al. 2018). The Maximum Likelihood (ML) analysis was conducted in IQ-TREE v1.6.12 (Nguyen et al. 2015) using the best-fit model GTR + F + I + G4 for all three fragments (*16S*, cyt *b*, and *ND4*), as determined by ModelFinder for IQ-Tree in PhyloSuite 1.2.3 according to Akaike information criterion (AIC) (Akaike 1973; Akaike 1974; Kalyaanamoorthy et al. 2017; Zhang et al. 2020). Node support was assessed using both the Ultrafast Bootstrap

Table 1. NCBI / DDBJ / NGDC accession numbers, localities, and voucher information for all specimens used in this study. * = DDBJ Accession Number, and # = NGDC Accession Number.

NO.	Species name	Locality	Voucher NO.	*16S*	cyt *b*	*ND4*	References
Genus *Trimeresurus*							
Subgenus *Viridovipera*							
1	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025027	LC899328*	LC899334*	LC899341*	This study
2	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025028	LC899329*	LC899335*	LC899342*	This study
3	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025029	LC899330*	LC899336*	LC899343*	This study
4	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025030	LC899331*	LC899337*	LC899344*	This study
5	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025031	LC899332*	LC899338*	LC899345*	This study
6	*Trimeresurus loong* sp. nov.	Anning, Kunming, Yunnan, China	QHU R2025032	LC899333*	LC899339*	LC899346*	This study
7	*T.* cf. *loong*	Huili, Sichuan, China	GP 37	EU443812	EF597522	EF597527	Dawson et al. (2008)
8	*T.* cf. *loong*	Huili, Sichuan, China	GP 38	EU443814	EF597523	EF597528	Dawson et al. (2008)
9	*Trimeresurus* sp.	Mt. Emei, Sichuan, China	CIB CB2120	C_AA122998.1#	C_AA122989.1#	C_AA123004.1#	Unpublished
10	*Trimeresurus* sp.	Mt. Yuping, Sichuan, China	CIB CB2121	C_AA122999.1#	C_AA122990.1#	C_AA123005.1#	Unpublished
11	*Trimeresurus* sp.	Mt. Emei, Sichuan, China	CIB CB2127	C_AA123000.1#	C_AA122991.1#	C_AA123006.1#	Unpublished
12	*T. mayaae*	Champhai, Mizoram, India	NCBS NRC-AA-0012	–	OM966859	–	Rathee et al. (2022)
13	*T. mayaae*	Ri-Bhoi, Meghalaya, India	BNHS 3658	–	OM966860	–	Rathee et al. (2022)
14	*T. mayaae*	Ri-Bhoi, Meghalaya, India	VR/ERS/ZSI/833	–	OM966862	–	Rathee et al. (2022)
15	*T. mayaae*	Manipur, India	MZMU 2970	–	OQ968476	–	Elangbam et al. (2023)
16	*T. mayaae*	Manipur, India	MZMU 2971	PP566116	–	–	Elangbam et al. (2023)
17	*T. medoensis*	Motuo, Xizang, China	SYS r001831 / CHS 824	MK194252	MK201553	–	Li et al. (2020)
18	*T. medoensis*	Motuo, Xizang, China	KIZ YPX46122	MW020095	MW111479	–	Che et al. (2020)
19	*T. medoensis*	Motuo, Xizang, China	KIZ YPX46123	MW020331	MW133479	–	Che et al. (2020)
20	*T. medoensis*	Motuo, Xizang, China	ANU ZR24025	–	PX068371	PX094008	This study
21	*T. medoensis*	Motuo, Xizang, China	ANU ZR24026	–	PX068372	PX094007	This study
22	*T. medoensis*	Motuo, Xizang, China	ANU ZR24072	–	PX068373	–	Xu et al. (2025)
23	*T.* cf. *medoensis*	Putao, Kachin, Myanmar	AM B416 / CAS 221528	AY352735	AY352765	AY352831	Malhotra and Thorpe (2004a)
24	*T.* cf. *medoensis*	Northeast India	V18	MG995794	MG995819	MG995834	Unpublished
25	*T. nujiang*	Fugong, Yunnan, China	ANU ZR24133	PX061893	PX068374	PX094009	Xu et al. (2025)
26	*T. nujiang*	Gongshan, Yunnan, China	CIB DLR353	PV994716	PX021391	PX021401	Liang et al. (2025)
27	*T. nujiang*	Gongshan, Yunnan, China	CIB DLR365	PX021397	PX021407	PV994722	Liang et al. (2025)
28	*T. nujiang*	Gongshan, Yunnan, China	CIB DLR375	PX021398	PX021408	PV994723	Liang et al. (2025)
29	*T. nujiang*	Gongshan, Yunnan, China	CIB DLR380	PX021399	PX021409	PV994724	Liang et al. (2025)
30	*T. pretiosus*	Yadong, Xizang, China	QHU R2025019	PX061894	PX068368	PX094011	Xu et al. (2025)
31	*T. pretiosus*	Yadong, Xizang, China	QHU R2025020	PX061895	PX068369	PX094010	Xu et al. (2025)
32	*T. pretiosus*	Yadong, Xizang, China	QHU R2025021	PX061896	PX068370	PX094012	Xu et al. (2025)
33	*T. stejnegeri*	Mt. Wuyi, Fujian, China	GP 816	–	KX019140	KX019294	Guo et al. (2016)
34	*T. stejnegeri*	Mt. Jinggang, Jiangxi, China	GP 662	–	KX019120	KX019274	Guo et al. (2016)
35	*T. stejnegeri*	Qimen, Anhui, China	GP 470	–	KX019094	KX019248	Guo et al. (2016)
36	*T. stejnegeri*	Jinhua, Zhejiang, China	GP 633	–	KX019111	KX019265	Guo et al. (2016)

NO.	Species name	Locality	Voucher NO.	*16S*	cyt *b*	*ND4*	References
37	*T. stejnegeri*	Youxi, Fujian, China	GP 755	–	KX019131	KX019285	Guo et al. (2016)
38	*T. stejnegeri*	Dehua, Fujian, China	GP 2435	–	KX019054	KX019209	Guo et al. (2016)
39	*T. stejnegeri*	Taichung, Taiwan, China	AM TST23	–	AF277689	EU443799	Creer et al. (2003); Dawson et al. (2008)
40	*T. stejnegeri*	Mt. Diaoluo, Hainan, china	GP 45	–	KX019088	KX019242	Guo et al. (2016)
41	*T. stejnegeri*	Qiongzhong, Hainan, China	GP 46	–	KX019089	KX019243	Guo et al. (2016)
42	*T. stejnegeri*	Qiongzhong, Hainan, China	GP 48	–	KX019104	KX019258	Guo et al. (2016)
43	*T. stejnegeri*	Cat Ba NP, Hai Phong, Vietnam	GP 881	–	KX019145	KX019299	Guo et al. (2016)
44	*T. stejnegeri*	Phia Oac-Phia Den NP, Cao Bang, Vietnam	ROM 35321	–	KT216408	KT216457	Guo et al. (2016)
45	*T. stejnegeri*	Nonggang, Guangxi, China	GP 2461	–	KX019056	KX019211	Guo et al. (2016)
46	*T. stejnegeri*	Nanchuan, Chongqing, China	GP 1227	–	KX019007	KX019162	Guo et al. (2016)
47	*T. stejnegeri*	Leishan, Guizhou, China	GP 1887	–	KX019034	KX019189	Guo et al. (2016)
48	*T. stejnegeri*	Luoding, Guangdong, China	KIZ 09939	–	KX019158	KX019312	Guo et al. (2016)
49	*T. stejnegeri*	Enshi, Hubei, China	GP 2011	–	KX019040	KX019195	Guo et al. (2016)
50	*T. truongsonensis*	Phong Nha-Ke Bang NP, Quang Tri Vietnam	AM B659 / VNUH 190606	EU443818	EU443815	EU443816	Dawson et al. (2008)
51	*T. truongsonensis*	Khammouane, Laos	NAP-09115	–	PX068365	PX094015	Xu et al. (2025)
52	*T. vogeli*	Nakhon Ratchasima, Thailand	AM B97	AY059562	AY059574	AY059596	Malhotra and Thorpe (2004a)
53	*T. vogeli*	Nakhon Ratchasima, Thailand	NAP-08227	–	PX068366	PX094013	Xu et al. (2025)
54	*T. vogeli*	Nakhon Ratchasima, Thailand	NAP-08228	–	PX068367	PX094014	Xu et al. (2025)
55	*T. yunnanensis*	Tengchong, Yunnan, China	QHU R2025033	LC899641*	LC899340*	LC899347*	This study
56	*T. yunnanensis*	Loei, Thailand	AM A164	AF517181	AY352766	AF517224	Malhotra and Thorpe (2004a); Creer et al. (2003)
57	*T. yunnanensis*	Pu Mat NP, Nghe An, Vietnam	AM B174	AY059563	AY059573	AY059595,	Malhotra and Thorpe (2004b)
58	*T. yunnanensis*	Jingdong, Yunnan, China	GP 851	–	KT216392	KT216441	Guo et al. (2015)
59	*T. yunnanensis*	Lincang, Yunnan, China	GP 3507	KT216339	KT216384	KT216433	Guo et al. (2015)
60	*T. yunnanensis*	Lincang, Yunnan, China	GP 3509	KT216341	KT216386	KT216435	Guo et al. (2015)
61	*T. yunnanensis*	Longling, Yunnan, China	KIZ 05089	KT216352	KT216399	KT216448	Guo et al. (2015)
62	*T. yunnanensis*	Jingdong, Yunnan, China	KIZ 047083	KT216351	KT216398	KT216447	Guo et al. (2015)
63	*T.* cf. *yunnanensis*	Honghe, Yunnan, China	GP 2532	KT216331	KT216376	KT216425	Guo et al. (2015)
64	*T.* cf. *yunnanensis*	Pingbian, Yunnan, China	GP 3273	KT216334	KT216379	KT216428	Guo et al. (2015)
65	*T.* cf. *yunnanensis*	Pingbian, Yunnan, China	GP 3275	KT216336	KT216381	KT216430	Guo et al. (2015)
66	*T.* cf. *yunnanensis*	Mengzi, Yunnan, China	GP 3564	KT216344	KT216389	KT216438	Guo et al. (2015)
67	*T.* cf. *yunnanensis*	Mengzi, Yunnan, China	GP 3589	KT216345	KT216390	KT216439	Guo et al. (2015)
Subgenus *Himalayophis*							
68	*T. arunachalensis*	Northeast India	APF/SFRI-1871	MK722155	MK720609	–	Captain et al. (2019)
69	*T. tibetanus*	Nepal	AM B258	AY352715	AY352749	AY352810	Malhotra and Thorpe (2004a)
Subgenus *Parias*							
70	*T. flavomaculatus*	Mindanao, Philippines	AM B4	AY352734	AY352764	AY352830	Malhotra and Thorpe (2004a)

NO.	Species name	Locality	Voucher NO.	*16S*	cyt *b*	*ND4*	References
71	*T. hageni*	Songhkla, Thailand	AM B33	AY059552	AY059567	AY059585	
72	*T. malcolmi*	Mt. Kinabalu, Sabah, Malaysia	AM B349	AY371786	AY371832	AY371861	Malhotra and Thorpe (2004a)
73	*T. mcgregori*	Batan Is., Philippines	AM B289	AY371795	AY371831	AY371858	Malhotra and Thorpe (2004a)
74	*T. schultzei*	Palawan, Philippines	AM B210	AY352725	AY352756	AY352819	Malhotra and Thorpe (2004a)
75	*T. sumatranus*	Bengkulu, Sumatra, Indonesia	AM B367	AY371791	AY371824	AY371864	Malhotra and Thorpe (2004a)
Subgenus *Sinovipera*							
76	*T. sichuanensis*	Sichuan, China	GP7 / YBU030116	HQ850449	HQ850447	HQ850446	Guo and Wang (2011)
Subgenus *Popeia*							
77	*T. lanna*	Doi Inthanon NP, Chiangmai, Thailand	AUP-00061	OR471637	OR470571	OR470534	Idiiatullina et al. (2024b)
78	*T. nebularis*	Cameron Highlands, Pahang, Malaysia	AM B345	AY371775	AY371811	AY371849	Sanders et al. (2006)
79	*T. phuketensis*	Phang Nga, Thailand	AM B467	AY371781	AY371807	AY371851	Sanders et al. (2006)
80	*T. popeiorum*	Yingjiang, Yunnan, China	DL2017070101	MH779887	MH779875	MH779879	Chen et al. (2019)
81	*T. sabahi sabahi*	Mt. Kinabalu, Sabah, Malaysia	AM B344	AY371771	AY371815	AY371842	Malhotra and Thorpe (2004a)
82	*T. tenasserimensis*	Suan Phueng, Ratchaburi, Thailand	ZMMU Re-17669	PP032802	OR999089	PP032781	Idiiatullina et al. (2024b)
Subgenus *Trimeresurus*							
83	*T. albolabris*	Shek Kwu Chan, Hong Kong, China	AM A157	AY352744	AF171884	AY352839	Malhotra and Thorpe (2000, 2004a)
84	*T. cantori*	Nicobar Is., India	AM A85	AY352741	AF171889	AY352836	Malhotra and Thorpe (2000, 2004a)
85	*T. caudornatus*	Yingjiang, Yunnan,China	AR1238	MK575042	MK575036	MK575038	Chen et al. (2020)
86	*T. ciliaris*	Thum Khao Ting, Trang, Thailand	ZMMU Re-17661	OR471621	OR470557	OR470538	Idiiatullina et al. (2023)
87	*T. erythrochloris*	Tham Si Va Cave, Klong Hat, Sa Kaeo, Thailand	RIM-0079	PQ654052	PQ658816	PQ658818	Pawangkhanant et al. (2025)
88	*T. ayeyarwadyensis*	Rangoon, Myanmar	AM A209	AF517174	AF171900	AF517217	Creer et al. (2003)
89	*T. kanburiensis*	Khao Yai NP, Kanchanaburi, Thailand	ZMMU Re-17667	–	OR470579	OR470553	Idiiatullina et al. (2023); Idiiatullina et al. (2024a)
90	*T. macrops*	Bangkok, Thailand	ZMMU Re-17856	–	PP766219	PP779475	Idiiatullina et al. (2024c)
Out group							
91	*Craspedocephalus puniceus*	Indonesia	AM B213	AF517177	AF517192	AF517220	Creer et al. (2003)
92	*Peltopelor malabaricus*	Tamil Nadu, India	AM A218	AY059564	AY059569,	AY059587	Malhotra and Thorpe (2004a)

Approximation (UFB) and the SH-like approximate likelihood ratio test (SH). UFB values were calculated with 5000 bootstrap replicates, with values ≥ 95% considered strong support; and SH was conducted with 1000 replicates, and values ≥ 80% were regarded as well supported (Stephane et al. 2010; Hoang et al. 2018). The Bayesian Inference (BI) analysis was conducted via MrBayes v3.2.7a (Ronquist et al. 2012) under the best-fit model GTR + F + I + G4 for all three fragments (*16S*, cyt *b*, and *ND4*), which was calculated according to BIC as well by ModelFinder for Mr-Bayes in PhyloSuite 1.2.3 (Zhang et al. 2020). In the BI analysis, three independent runs were conducted with 1 × 107 generations and sampled every 1000 generations, with the first 25% of samples discarded as burn-in. Nodes with Bayesian posterior probabilities (PP) ≥ 0.95 were considered strongly supported (Huelsenbeck et al. 2001). The phylogenetic tree was visualized using FigTree v.1.4.4 (Rambaut 2018). Uncorrected pairwise genetic distances (*p*-distances) among species were also calculated using MEGA X (Kumar et al. 2018).

Morphological and hemipenial examination

A total of 31 morphological characters were recorded for each specimen (following Vogel et al. 2023; Xu et al. 2025). Measurements were taken with a Mitutoyo digital calipers (CD-15AX) to the nearest 0.1 mm, except for body and tail lengths, which were measured to the nearest millimetre with a measuring tape. The number of ventral scales was counted according to Dowling (1951). Half ventrals were counted as one. The first enlarged shield

anterior to the ventrals was regarded as a preventral and was present in all examined specimens. The first scale under the tail meeting its opposite was regarded as the first subcaudal, and the terminal scute was not included in the number of subcaudals. The dorsal scale rows were counted at one head length behind the head, at mid-body, and at one head length before the vent. In the number of supralabials touching the subocular, those only touching the presubocular were not included. Infralabials were considered to be those shields that were completely below a supralabial and bordering the mouth gap. The first sublabial was defined as the scale that starts between the posterior chin shield and the infralabials and that borders the infralabials. Values for paired head characters were recorded on both sides of the head and were reported in a left-right order. In addition, we paid special attention to diagnostic color pattern characters, such as eye color, postocular streak, ventrolateral stripe, tail coloration, and overall body coloration. The sex was determined by dissection of the ventral tail base.

Comparative morphological data were compiled from the literature, including Schmidt (1925,1927), Maki (1931), Pope (1935), Zhao et al. (1998), David et al. (2001a, b, 2002), Ao et al. (2004), Orlov et al. (2004), David and Mathew (2005), Zhao (2006), Guo et al. (2009), Teynié and David (2014), Nguyen et al. (2018), Che et al. (2020), Rathee et al. (2022), Elangbam et al. (2023), Nguyen et al. (2025), Liang et al. (2025), and Xu et al. (2025).

Hemipenial morphology

The preparation, measurement, and description of hemipenes followed the methodologies of Zhang et al. (1984), Myers and Cadle (2003), Jiang (2010), and Ren et al. (2022, 2025). Hemipenial material was obtained from the left side of fresh or preserved adult male specimens. Everted hemipenes were reinflated using colored petroleum jelly, and images were captured using a digital camera.

The measurement characters of the hemipenis are as follows: **HTL** = hemipenial total length; **HTW** = hemipenial total width; **HCL** = hemipenial truncus length; and **SPBD** = sulcus spermaticus bifurcation distance, measured from the base of the hemipenis to the bifurcation point of the sulcus spermaticus in the vertical direction. The following ratios were used for comparative purposes: **HCL/HTL** = ratio of truncus length to total length; and **SPBD/HCL** = ratio of sulcus bifurcation distance to truncus length, to evaluate the relative position of the sulcus bifurcation point along the hemipenial truncus.

Specimen information of *Viridovipera* species used in hemipenial comparisons conducted in this study are provided below:

Trimeresurus medoensis (N = 1): QHU R2025040 (adult male), collected on June 2018, by Jundong Deng, from Beibeng Township, Motuo (Medog) County, Nyingchi City, Xizang Autonomous Region, China (approx. 29.23°N, 95.18°E).

Trimeresurus pretiosus (N = 2): QHU R2025019 (adult male), collected on 22 June 2025 by Zhenqi Wang, Yuhao Xu, Fanyue Sun, and Lifang Peng, from Xiayadong Township, Yadong County, Xigaze City, Xizang Autonomous Region, China (27.262°N, 89.016°E; elevation 1824 m asl.); QHU R2025020 (adult male), collected on 22 June 2025, shares the same locality and collector as QHU R2025019.

Trimeresurus stejnegeri (N = 1): QHU R2025037 (adult male), collected on September 2025 by Yuhao Xu, from Liandu District, Lishui City, Zhejiang Province, China (28.499°N, 119.922°E; elevation 526 m asl.).

Trimeresurus yunnanensis (N = 1): QHU R2025035 (adult male), collected on July 2025 by Jundong Deng, from Lincang City, Yunnan Province, China (approx. 23.91°N, 100.15°E).

Abbreviations

Morphological descriptions and morphometry follow standardized abbreviations revised according to Darko et al. (2022). The morphometric characters are as follows: **SVL** = snout-vent length; **TAL** = tail length; **TL** = total length; **TAL/TL** = ratio of tail length to total length; **HL** = head length; **HW** = head width; **ESD** = eye-snout distance, measured from the tip of the snout to the anterior edge of eye; **ED** = eye diameter; **EN** = eye to nostril distance, measured from the anterior margin of the eye to the posterior margin of the nostril; **SOL** = subocular length; and **SOW** = subocular width.

The scalation characters are as follows: **VS** = number of ventral scales; **SC** = number of subcaudal scales; **CP** = cloacal plate; **SL** = supralabials; **IL** = infralabials; **DSR** = dorsal scale rows; **ASR** = anterior dorsal scale rows; **MSR** = dorsal scale rows at midbody; **PSR** = posterior dorsal scale rows; **PRO** = preoculars; **PO** = postoculars; **SO** = supraocu-lars; **SBO** = suboculars; **IOS** = interorbital scales, number of scales at the narrowest point between the orbits; **SpOC** = number of dorsal head scales surrounding the supraocular; **NS** = Nasals; **INS** = internasals; **NINN** = number of scales separating the internasals; **KTEM** = keeling of the temporal scales, and **KOCC** = keeling of the occipital scales.

Other abbreviations: **AR** = Autonomous region; **NP** = National Park; **NR** = Nature Reserve; **Mt** = Mountains; **asl.** = above sea level; **WS** = Wildlife Sanctuary.

Result

Phylogenetic relationships

The concatenated sequence alignment was 2,314 base pairs (bp) in length (*16S* = 508 bp; cyt *b* = 1,034 bp; and *ND4* = 772 bp). Both ML and BI analyses yielded congruent topologies (Fig. 2). According to our mtDNA-based phylogeny, all putative *Trimeresurus* species cluster into a single clade. However, relationships among species within

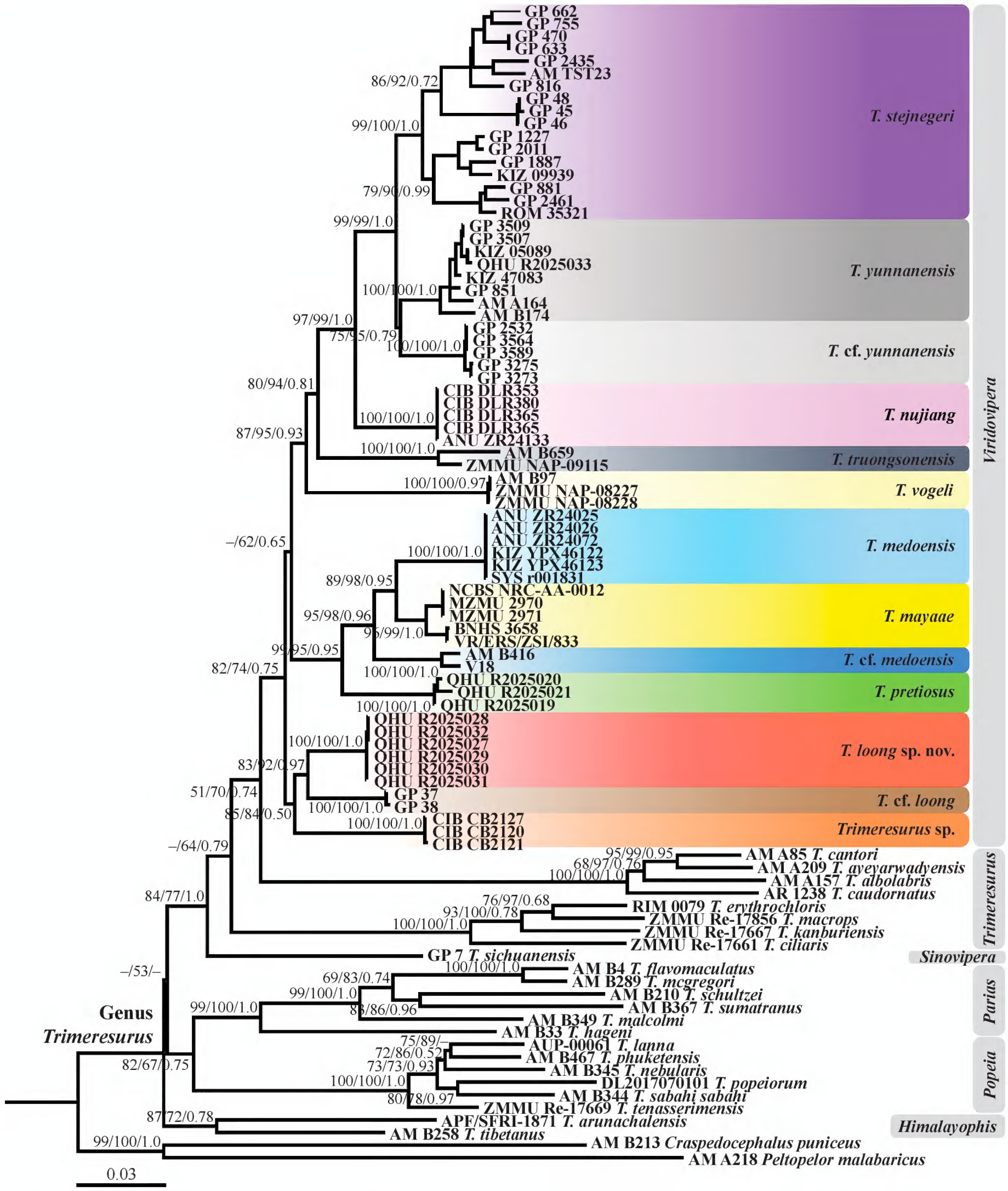

Figure 2. Phylogram of the genus *Trimeresurus* inferred from three mitochondrial (*16S*/cyt *b*/*ND4*) fragments. The branch support values are presented with the SH-like approximate likelihood ratio test (SH)/Ultrafast Bootstrap Approximation (UFB)/Bayesian posterior probabilities (PP); the ones lower than 50 or 0.5 are displayed as "–".

the genus remain poorly resolved. The monophyly of the subgenera *Parias* and *Popeia* was strongly supported (SH 99/ UFB 100 / PP 1.0; SH 100 / UFB 100 / PP 1.0 respectively), while subgenus *Himalayophis* and *Viridovipera* received moderate support (SH 87 / UFB 72 / PP 0.78; SH 82 / UFB 74 / PP 0.75, respectively). The subgenus *Trimeresurus* is not recovered as monophyletic in analysis and is clearly divided into two deeply divergent clades.

Within the subgenus *Viridovipera*, phylogenetic relationships among species are generally well resolved (Fig. 2). Two specimens AM B416 (= CAS 221528) from Kachin State, Myanmar and V18 from Northeast India, previously identified as *T. medoensis*, form a distinct clade that is sister to the clade comprising *T. medoensis* and *T. mayaae*. Therefore, we tentatively refer to these specimens as *T.* cf. *medoensis*. In addition, five specimens

from southeastern Yunnan Province, China (GP 2532, GP 3273, GP 3275, GP 3564, and GP 3589), previously identified as *T. gumprechti*, form a sister clade to *T. yunnanensis* with moderate support (SH = 75 / UFB = 97 / PP = 0.79). The uncorrected *p*-distances between the two clades range from 4.0–6.2% for cyt *b* and 2.9–5.1% for *ND4*. As morphological data for this population are not yet available, we tentatively refer to these specimens as *T.* cf. *yunnanensis*. The six unidentified *Trimeresurus* specimens from Anning, Kunming City, Yunnan Province form a well-supported monophyletic clade (SH = 100 / UFB = 100 / PP = 1.0). This clade is sister to two specimens from Huili City, Sichuan Province (GP 37 and GP 38), which had long been misidentified as *T. yunnanensis*. Together, they form a distinct subclade with three additional specimens from western Sichuan Province (CIB CB2120, CIB CB2121, and CIB CB2127), with moderate support in the ML analysis (SH = 85 / UFB = 84), but low support in the BI analysis (PP = 0.5). This entire assemblage clusters at the outer margin of the clade formed by all other currently recognized species of *Viridovipera*.

Uncorrected *p*-distances for the cyt *b* and *ND4* gene fragments are summarized in Table 2 and Table 3, respectively. Among currently recognized *Viridovipera* species, interspecific genetic distances ranged from 4.9% (*T. stejnegeri* and *T. yunnanensis*) to 12.8% (*T. vogeli* and *T. yunnanensis*) for the cyt *b* gene (Table 2), and from 3.1% (*T. stejnegeri* and *T. yunnanensis*) to 11.0% (*T. pretiosus* and *T. vogeli*) for the *ND4* gene (Table 3). The Anning population exhibited substantial genetic divergence from all other recognized congeners, with uncorrected *p*-distances ranging from 6.7% (vs. *T. mayaae*) to 11.2% (vs. *T. stejnegeri*) for the *cyt b* gene, and from 6.1% (vs. *T. yunnanensis*) to 8.3% (vs. *T. medoensis*) for the *ND4* gene. In addition, specimens from Huili City, Sichuan Province showed cyt *b* divergence of 4.8–4.9% and *ND4* divergence of 4.1–5.2% from the specimens from Anning, Yunnan Province. These values approach the minimum interspecific divergence observed within *Viridovipera* for cyt *b*, and exceed the minimum observed for *ND4*. Meanwhile, specimens from western Sichuan Province differed from the Anning population by 7.0–7.1% in cyt *b* and 5.9–6.1% in *ND4*, clearly exceeding the minimum interspecific distances within the subgenus.

Liang et al. (2025) assessed the taxonomic status of *Trimeresurus gumprechti* David, Vogel, Pauwels & Vidal [type locality: Phu Luang WS, Loei Province, Thailand], based on four mitochondrial gene fragments (*12S*, *16S*, cyt *b*, and *ND4*) together with morphological data. Their analyses revealed that the topotypes of *T. gumprechti* clustered with the topotypes of *T. yunnanensis*, and that the genetic divergence between the two (0.0–1.6% in cyt *b*) was markedly lower than typical interspecific divergence within the subgenus *Viridovipera*. Consequently, *T. gumprechti* was treated as a junior synonym of *T. yunnanensis*. Our phylogenetic analyses yielded similar results in this regard. However, the phylogenetic topology presented by Liang et al. (2025) placed the subgenus *Trimeresurus* nested within what was previously considered the subgenus *Viridovipera*, forming a sister group to *T. medoensis*, *T. mayaae*, and *Trimeresurus* sp. (Huili City, Sichuan Province, China). Based on this result, they annotated *Viridovipera* on their phylogenetic tree as comprising only the clade including *T. stejnegeri*, *T. yunnanensis*, *T. vogeli*, *T. truongsonensis*, and *T. nujiang*, thereby excluding *T. medoensis*, *T. mayaae*, and *Trimeresurus* sp. (Huili City, Sichuan Province, China) from the subgenus. This arrangement is incongruent with both previous studies and our own morphological and molecular evidence (Creer et al. 2003; Malhotra and Thorpe 2004a, b; Dawson et al. 2008; Guo et al. 2015, 2016; Rathee et al. 2022; Xu et al. 2025; this study). A likely explanation for this inconsistency is that Liang et al. (2025) included only three species of the subgenus *Trimeresurus*, namely *T. septentrionalis* Kramer, 1977, *T. guoi*, and *T. purpureomaculatus* (Gray, 1832), and the phylogenetic resolution in this part of the tree is rather weak. Therefore, the overall phylogenetic framework proposed by Liang et al. (2025) warrants additional verification with expanded sampling.

Furthermore, detailed morphological examinations confirmed that the specimens from Anning, Kunming, Yunnan are diagnosably distinct from all known *Viridovipera* species. However, due to the lack of available morphological data for the Huili and Chengdu in Sichuan Province specimens, we are currently unable to determine their exact taxonomic status. Based on the combined molecular and morphological evidence, we describe the population from Anning City, Kunming City, Yunnan Province, China as a new species, and the Huili population is tentatively reassigned to this new species, while the western Sichuan population is herein treated as *Trimeresurus* sp.

Taxonomy

***Trimeresurus loong* Xu, Deng, Zhang, Nguyen, Poyarkov, Vogel & Peng, sp. nov.**

https://zoobank.org/B557FA3A-3B3A-47C2-A9F8-239824C7DE63

Tables 4, 5; Figs 3, 4A, B, 5–8, 9B, C, 10A, B, 11A1, A2

Type material. ***Holotype*** • QHU R2025027, adult male, collected from Qinglongxia, Anning City, Kunming City, Yunnan Province, China (25.0590°N, 102.3561°E; elevation 1,822 m asl.), on 15 September 2025 by J.D. Deng and Y.H. Xu.

***Paratypes* (n = 5)** • QHU R2025031 (adult female), with same data as the holotype. • QHU R2025028 (adult male), collected on 22 September 2025 by J.D. Deng and Y.H. Xu; • QHU R2025029 (subadult male) and • QHU R2025032 (adult female), collected on 27 May 2025 by J.D. Deng; • QHU R2025030 (subadult male), collected on 21 September 2025 by J.D. Deng and Y.H. Xu; all from the same locality as the holotype.

Diagnosis. The new species *Trimeresurus loong* sp. nov. is distinguished from all of its congeners by a combination of the following morphological characters: (1) first

Table 2. Uncorrected *p*–distances (%) between the sequences of cyt *b* gene of species of the subgenus *Viridovipera* included in the phylogenetic analyses. The values represent the minimum and maximum observed genetic divergence between species.

NO.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*T. loong* sp. nov.	0.0												
2	*T.* cf. *loong*	4.8–4.9	0.1											
3	*Trimeresurus* sp.	7.0–7.1	7.1–7.5	0.0–0.1										
4	*T. mayaae*	6.7–7.1	7.1–7.4	7.7–8.4	0.0–1.5									
5	*T.* cf. *medoensis*	6.7–7.2	7.1–7.3	6.5–7.8	4.4–5.1	2.2								
6	*T. medoensis*	7.7–8.3	8.4–9.0	8.3–9.8	5.1–5.9	6.7–6.9	0.0							
7	*T. nujiang*	7.5–7.6	7.4–7.8	7.9–8.0	8.1–8.5	7.2–7.7	8.3–9.5	0.0						
8	*T. pretiosus*	7.2–7.7	7.7–7.8	7.6–7.9	5.9–7.0	5.8–6.3	6.5–7.5	7.9–8.2	0.2–0.5					
9	*T. stejnegeri*	8.0–11.2	8.0–11.2	9.3–11.6	8.1–11.6	8.1–12.1	8.2–11.7	6.4–8.2	9.3–12.1	0.1–7.5				
10	*T. truongsonensis*	8.0–9.1	7.5–9.3	8.8–10.5	8.8–9.4	8.5–9.0	9.3–10.7	7.6–8.5	9.3–10.5	7.6–10.6	3.3			
11	*T. vogeli*	7.8–8.4	9.1–9.5	10.2–10.6	8.7–10.2	8.8–9.9	9.2–11.0	8.3–9.5	10.5–11.9	9.6–12.8	9.2–10.9	0.1–0.2		
12	*T. yunnanensis*	8.5–10.3	9.0–10.6	8.4–10.3	9.5–2.1	9.2–11.0	10.1–12.4	5.7–7.6	9.0–10.7	4.9–7.9	6.9–10.5	9.3–12.8	0.1–3.5	
13	*T.* cf. *yunnanensis*	8.4–8.9	8.8–9.5	7.7–9.1	8.2–10.2	7.5–8.8	10.0–11.5	6.4–6.7	8.1–9.8	4.4–6.5	7.4–9.3	9.6–11.5	4.0–6.2	0.0–0.4

Table 3. Uncorrected *p*–distances (%) between the sequences of *ND4* gene of species of the subgenus *Viridovipera* included in the phylogenetic analyses. The values represent the minimum and maximum observed genetic divergence between species.

NO.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	*T. loong* sp. nov.	0.0–0.2											
2	*T.* cf. *loong*	4.1–5.2	0.2										
3	*Trimeresurus* sp.	5.9–6.1	5.5–6.5	0.0									
4	*T.* cf. *medoensis*	7.9–8.3	7.0–7.4	8.5–8.7	0.0								
5	*T. medoensis*	8.1–8.3	7.4–8.6	7.8	6.5–6.8	0.0							
6	*T. nujiang*	6.2–6.4	6.6–7.0	8.6–8.7	8.7–9.1	9.4–9.5	0.0						
7	*T. pretiosus*	7.6–7.7	6.7–7.4	8.8	7.8–7.9	7.0	8.2	0.0					
8	*T. stejnegeri*	6.2–8.1	5.8–8.8	7.5–8.7	7.6–10.4	8.1–9.3	5.5–7.8	7.8–9.1	0.0–6.3				
9	*T. truongsonensis*	6.4–6.8	6.8–7.3	6.7–7.9	8.5–8.9	9.3–10.3	7.4–8.3	9.1–10.0	6.7–9.5	2.2			
10	*T. vogeli*	6.8–7.3	7.9–8.2	7.4–8.0	11.4–12.1	9.6–10.3	8.2–8.6	10.1–11.0	7.1–9.5	7.2–8.7	0.0–0.2		
11	*T. yunnanensis*	6.1–7.4	6.0–7.7	7.7–8.5	8.9–10.3	8.0–9.5	4.9–5.8	8.3–9.4	3.1–6.0	7.3–8.7	7.6–8.7	0.0–2.0	
12	*T.* cf. *yunnanensis*	5.8–7.6	6.2–6.8	6.8–8.5	7.9–9.6	7.1–8.7	5.4–6.5	8.6–9.3	3.2–6.3	6.7–8.3	8.1–9.7	2.9–5.1	0.0–0.2

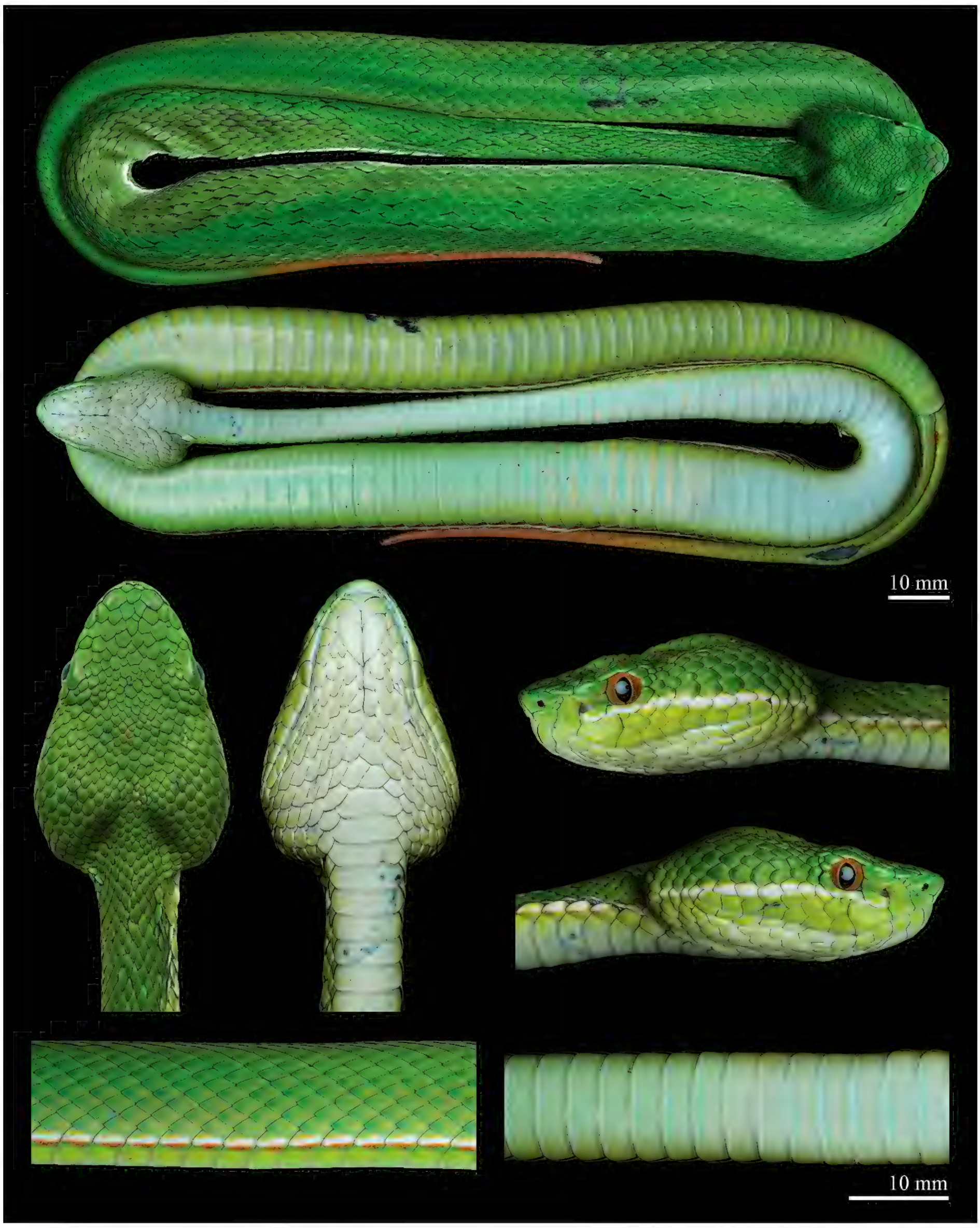

Figure 3. Fresh specimen of the holotype of *Trimeresurus loong* sp. nov. (QHU R2025027, adult male). Photographs by Y.H. Xu. Scale bars: 10 mm.

supralabial completely separated from the nasal scale; (2) hemipenis short and spinose, reaching the 10th–11th subcaudal when fully everted; (3) moderate adult body size, with a maximum SVL of 601 mm in males and 657 mm in females; (4) dorsal scales in 19 (21 or 23)–19–15 rows, keeled except for the outermost rows; (5) VS 150–151 in males and 157–158 in females; (6) SC 67–68 in males and 57–64 in females; (7) iris amber and sometimes exhibiting a faint reddish hue in adult males and yellowish in adult females; (8) body uniformly bright grass-green;

Figure 4. Comparisons of hemipenes within the subgenus *Viridovipera*, showing morphological differences on sulcus side, asulcate side, and apical side of hemipenis, from left to right. **A.** *Trimeresurus loong* sp. nov., QHU R2025027, holotype; **B.** *Trimeresurus loong* sp. nov., QHU R2025028, paratype; **C.** *T. medoensis*, QHU R2025040, from Motuo (Medog), Xizang, China; **D.** *T. pretiosus*, QHU R2025020, from Yadong, Xizang, China; **E.** *T. stejnegeri*, QHU R2025037, from Lishui, Zhejiang, China; **F.** *T. yunnanensis*, QHU R2025035, from Lincang, Yunnan, China. **SPBP:** sulcus spermaticus bifurcation point. Photographs by Y.H. Xu. Scale bars: 10 mm.

(9) postocular streak narrow and white, with a few scale margins slightly tinged with yellow or reddish-brown in males, and absent in females; (10) ventrolateral stripe along the first dorsal scale row, variable in coloration in males, occurring in two forms, the first is a narrow white band bordered dorsally by a faint yellowish margin and ventrally by a red line, with a diffuse brownish tinge below the red line; the second is a narrow white band bordered by faint yellowish margins; and in females, the stripe is absent or reduced, and almost entirely white when present; (11) the ventral surfaces pale yellowish white or pale greenish-yellow anteriorly; gradually transitioning to greenish-yellow or light green toward the posterior body; (12) tail distinctly bicolored dorsally, green anteriorly and becoming almost uniformly orange or light orange-red posteriorly.

Etymology. The specific epithet *loong* is a Latinized appositive noun derived from the Chinese word "龙" (*lóng*), meaning "loong" or "dragon." In Chinese culture, snakes are often regarded as "little dragons" or "lesser dragons" because of their serpentine form and symbolic association with the dragon (loong). The name also refers to the type locality, Qinglongxia (青龙峡), which literally translates to "Green Dragon Gorge." The vivid green coloration of the new species echoes this name, establishing both symbolic and geographical connections. In addition, the year 2025, which marks the discovery and collection of this species, corresponds to the Year of the Snake in the lunar calendar. We therefore propose the common names "昆明竹叶青蛇" (Kūn Míng Zhú Yè Qīng Shé) in Chinese and "Kunming Green Pit Viper" in English, referring to its type locality Kunming City, Yunnan Province, China.

Description of holotype. (Fig. 3) ***Morphology.*** Adult male in a good state of preservation. Body cylindrical and elongated, with SVL 517 mm, TAL 129 mm, and TL 646 mm; tail relatively long, TAL/TL ratio 0.20; head triangular, wide at base, clearly distinct from the neck, HL 25.8 mm, HW 17.7 mm, HH 9.8 mm, HW/HL ratio 0.69. Snout elongate, round anteriorly, ESD 8.6 mm, EN 5.4 mm, ESD/HL ratio 0.33. Eyes of moderate size, ED 3.3 mm, ED/ESD

ratio 0.38, and ED/HL ratio 0.13; pupil is vertically elliptical, becoming progressively narrower in brighter light and widening in dimmer conditions in live individual.

Head scalation. Rostral triangular, slightly visible from above; nasal single, undivided, completely separated from the first supralabial; nostril positioned centrally within the nasal scale; a pair of slightly enlarged internasals, separated from each other by two small anterior scales and one larger posterior scale; 3/4 canthal scales bordering the canthus rostralis between the internasal and corresponding supraocular. Loreal pit present, triangular in shape, located closer to eye than to nostril. PRO 3/3, elongate, two upper preoculars positioned above the loreal pit, both in contact with the single loreal, the lower preocular forms the lower margin of the loreal pit and contacts the 3rd supralabial; PO 2/2; SBO 1/1, long and crescent-like, contacting the 3rd supralabial, separated from the 4th–6th supralabial by two row of scales; SO 1/1, large, SOL 4.3 mm, SOW 1.9 mm. Scales on the dorsal surface of the snout enlarged, flat, smooth, and irregular in shape, gradually decreasing in size posteriorly; cephalic scales small, smooth, and irregularly shaped; IOS 9; temporal scales smooth and occipital scales very weakly keeled. SL 10/10, the 1st supralabial triangular; the 2nd is the tallest, with a concave upper part forming the anterior border of the loreal pit, completely separated from the nasal by two small scales; the 3rd widest, with the remaining supralabials gradually decreasing in size posteriorly; IL 12/11, the first pair in contact with each other behind the mental; the first two pairs in contact with the single pair of chin shields.

Body scalation. DSR 19-19-15; at midbody, all dorsal scale rows except the outermost are weakly keeled, with keels faint laterally and becoming more distinct toward the mid-dorsal rows. The outermost row is completely smooth. VS 150 (+2 preventrals); SC 67, paired; CP entire.

Hemipenis (Fig. 4). Described based on the everted left organ. When fully everted, the hemipenis is relatively short and robust, extending to the 11th subcaudal scale. Total length (HTL) 27.4 mm; total width (HTW) 12.9 mm. It is Y-shaped and bilaterally symmetrical, with truncus length (HCL) 18.0 mm, HCL/HTL ratio 0.66.

The basal one-fifth of the truncus is smooth. Above this region, a sparse ring of fine spines appears. These small spinules extend upward along the outer margin of the sulcus spermaticus, gradually increasing in size to form a row of slightly larger keratinized spines, which disappear halfway along the bifurcated region. These spines are arranged in a nearly symmetrical pattern on both sides, with 14 well-developed keratinized spines on the left and 18 on the right (excluding the smaller spines along the margin of the sulcus spermaticus). On the sulcate side, the area medial to the sulcus spermaticus corresponds to the calyx region, while the lateral area constitutes the spine region. On the asulcate side, the boundary between the spine and calyx regions is oblique and clearly demarcated; the calyculate region is restricted to the distal half of each branch. The sulcus spermaticus is divided and runs centrifugally, extending nearly to the tip of each branch. It bifurcates at a distance of 8.8 mm from the bottom of the hemipenis, with an SPBD/HCL ratio of 0.49. The sulcal lips are well developed but not prominently raised, and lack spinules.

Coloration of holotype in life (Fig. 5). The dorsal surface of the head and body is bright and grass-green, lacking crossbars or mottling, with a slightly paler tone along the sides that deepens toward the middle. The interstitial skin between the dorsal scales is relatively uniformly dark grayish-black or black, visible only when the body is inflated. A narrow postocular stripe, white with a faint yellowish margin, extends posteriorly from below the loreal pit, passes beneath the eye, and ultimately merges with a distinct, continuous ventrolateral stripe that runs along the first dorsal scale row from just behind the corner of the mouth to the cloacal plate, and continues as a broken line onto the anterior part of the tail. The ventrolateral stripe consists of a narrow white line occupying the center of the first dorsal scale row, bordered dorsally by a faint yellowish edge, and ventrally by a thin, red line, with a diffuse brownish tinge below the red line and the upper and lower margins of the scales remaining green.

The dorsal scales immediately above the stripe are bright green with fine creamish-blue speckling. The dorsal surface of the tail is distinctly bicolored, green in the anterior half and gradually suffused with nearly uniform light orange-red toward the distal half, with the tail tip blackish brown (Fig. 6A). The infralabials are light green, transitioning to light yellowish white toward the ventral surface of the head. On the anterior portion of the venter, the lateral edges are yellowish-green, while the center is creamish-yellow. Posterior to the midbody, the ventral surface becomes more uniformly light green or yellowish-green. The anterior portion of the ventral surface of the tail is pale green, while the posterior portion is orange-red. The iris is amber with a faint, almost imperceptible reddish tint and a subtle golden hue.

Coloration of the holotype in preservative. As the holotype had been preserved in alcohol for less than one month at the time of description, its coloration had not undergone any substantial change. Minor alterations were observed only in certain regions: the eyes turned pale gray, several lateral rows of dorsal scales had turned dull yellowish-green, and the small bluish-white speckles had gradually disappeared. The yellow upper margin of the ventrolateral stripe has disappeared, the central red line has become dull, and the stripe has changed to white with reddish-brown. The ventral surface of the head had gradually become pale creamish-yellow; the pale yellowish-green coloration along the lateral margins of the anterior ventral body had faded; and the central yellowish-white region had become even paler.

Variation. The main morphological characters of *Trimeresurus loong* sp. nov. are listed in Table 4. The longest known male specimen is 748 mm long (QHU R2025028 (paratype); SVL 516 mm, TAL 117 mm); and the only known female specimen with is 792 mm long (QHU R2025031 (paratype); SVL 657 mm, TAL 135 mm); TAL/TL ratio 0.19–0.20 in males, and 0.17–0.19 in females.

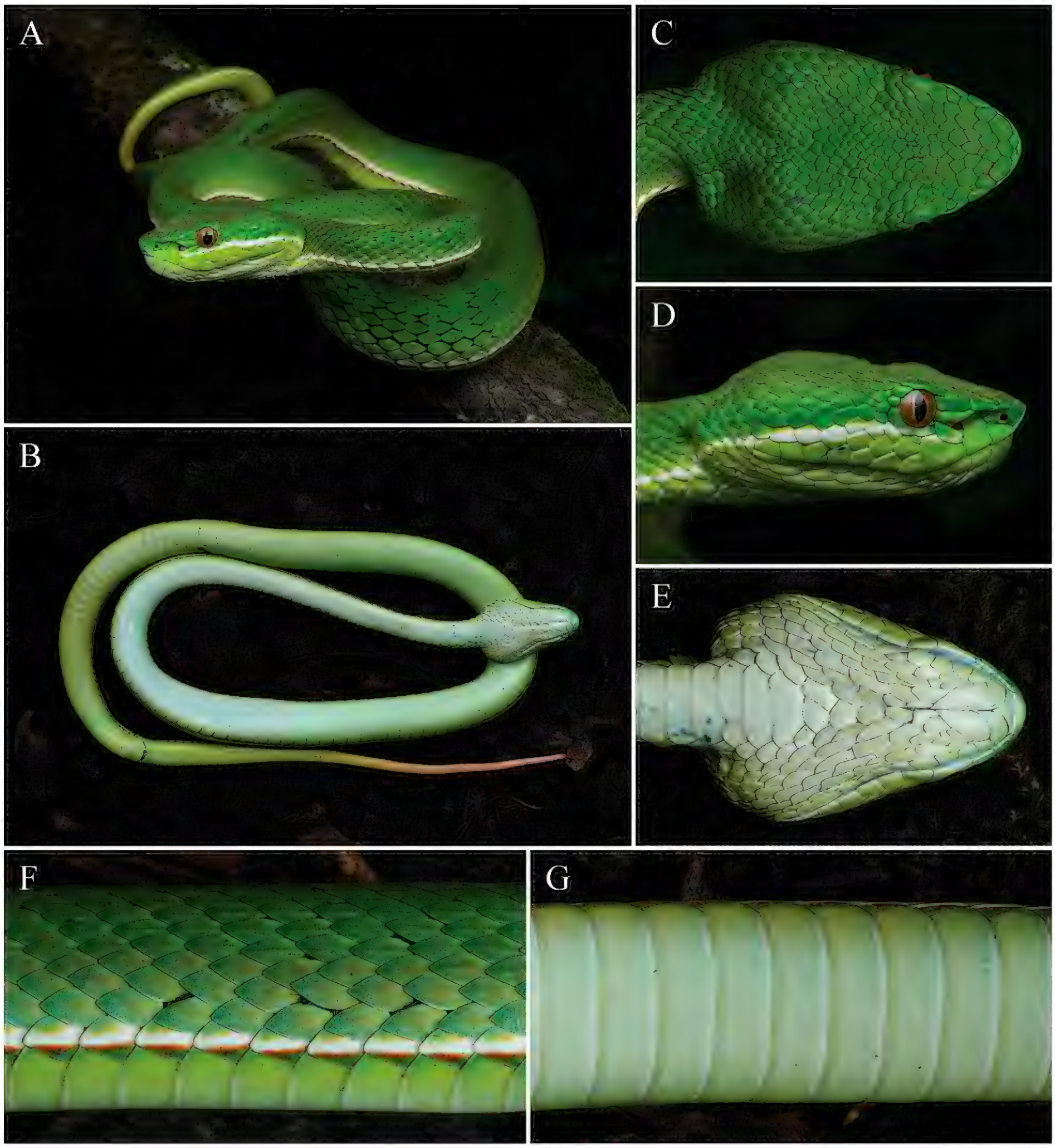

Figure 5. Coloration of the holotype of *Trimeresurus loong* sp. nov. in life (QHU R2025027, adult male). **A.** Dorsolateral view; **B.** Ventral view; **C.** Dorsal view of the head; **D.** Lateral view of the head; **E.** Ventral view of the head; **F.** Lateral view of the body; **G.** Ventral view of the body. Photographs by Y.H. Xu.

Scalation (Fig. 7). Nasal single, undivided; internasals slightly enlarged, separated by either juxtaposed scales, or by a combination of two small anterior scales and one larger posterior scale; SO usually 1/1, but in specimen QHU R2025028 the left supraocular is divided into three small scales and the right into two; temporal scales smooth; occipital scales are mostly weakly keeled, but smooth in specimens QHU R2025028 and QHU R2025032; IOS 7–11; PRO 3; PO 2–4; SL 10–11; IL 11–14. DSR (19–23)-19-15; at midbody, all dorsal scale rows except the outermost are weakly keeled, with keels faint laterally and becoming more distinct toward the mid-dorsal rows. The outermost row is completely smooth. VS 150–151 in males and 157–158 in females; SC 67–68 in males and 57–64 in females, paired; CP entire.

Main characters of hemipenis (Fig. 4A, B). The description is based on the everted organ of two male specimens (QHU R2025027 and QHU R2025028). When fully everted, the hemipenis is relatively short and robust, extending to the 10^{th}–11^{th} subcaudal scale. The hemipenis is Y-shaped and bilaterally symmetrical, the truncus is slightly longer than the branches, with HCL/HTL ratio 0.62–0.66.

Figure 6. Dorsal and ventral views of the tail of *Trimeresurus loong* sp. nov. **A.** QHU R2025027, holotype, adult male; **B.** QHU R2025028, paratype, adult male; **C.** QHU R2025029, paratype, subadult male; **D.** QHU R2025030, paratype, subadult male; **E.** QHU R2025031, paratype, adult female. Photographs by Y.H. Xu. Scale bars: 20 mm.

The basal one-fifth of the truncus is smooth. Above this region, a sparse ring of fine spines appears. These small spinules extend upward along the outer margin of the sulcus spermaticus, gradually increasing in size to form a row of slightly larger keratinized spines, which disappear halfway along the bifurcated region. These spines are arranged in a nearly symmetrical pattern, with 14–19 conspicuously enlarged spines of varying sizes on each side (excluding the smaller spines along the margin of the sulcus spermaticus). On the sulcate side, the area medial to the sulcus spermaticus corresponds to the calyx region, while the lateral area constitutes the spine region. On the asulcate side, the boundary between the spine and calyx regions is oblique and clearly demarcated; the calyculate region is restricted to the distal half of each branch. The sulcus spermaticus is divided and runs centrifugally, bifurcating near the midpoint of the truncus and extending nearly to the tip of each branch, with SPBD/HCL ratio of 0.43–0.49. The sulcal lips are well-developed but not prominently raised, and lack spinules.

Main characters of the pattern in life (Fig. 8). Coloration in life shows moderate variation among males,

Table 4. Main measurements and meristic characters of the type series of *Trimeresurus loong* sp. nov.

Specimen voucher	QHU R2025027	QHU R2025028	QHU R2025029	QHU R2025030	QHU R2025031	QHU R2025032
Type	Holotype			Paratype		
Sex	Male	Male	Subadult male	Subadult male	Female	Female
SVL (mm)	517	601	402	335	657	632
TAL (mm)	129	147	96	83	135	146
TL (mm)	646	748	498	418	792	778
TAL/TL	0.20	0.20	0.19	0.20	0.17	0.19
HL (mm)	25.8	29.0	20.7	19.3	36.6	34.6
HW (mm)	17.7	20.9	14.4	13.9	27.6	20.9
HW/HL	0.69	0.72	0.70	0.72	0.75	0.60
ESD (mm)	8.6	9.5	6.6	5.7	11.4	8.9
EN (mm)	5.4	6.6	4.5	4.0	7.7	6.7
ED (mm)	3.3	3.6	2.4	2.7	4.2	4.3
ED/ESD	0.38	0.38	0.36	0.47	0.37	0.48
ED/HL	0.13	0.12	0.12	0.14	0.11	0.12
NS	1, undivided	1, undivided	1, undivided	1, undivided	1, undivided	1, undivided
INS	Slightly enarged	Slightly enarged	Slightly enarged	Slightly enarged	Slightly enarged	Slightly enarged
NINN	2 small + 1 large	2 small + 1 large	2	2	2	2
PRO	3	3	3	3	3	3
PO	2/2	4/4	2/2	3/3	2/2	3/3
SO	1/1	3/2	1/1	1/1	1/1	1/1
SOL	4.3	–	3.6	3.4	5.4	4.3
SOW	1.9	–	1.3	1.2	2.1	2.1
SBO	1/1	1/1	1/1	1/1	1/1	1/1
IOS	9	10	7	9	10	11
SpOC	8/8	8/7	7/8	9/8	6/5	6/7
KTEM	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
KOCC	Slightly keeled	Smooth	Slightly keeled	Slightly keeled	Slightly keeled	Smooth
SL	10/10	11/10	10/10	10/10	11/11	10/10
IL	12/11	12/11	12/12	11/12	13/14	12/12
DSR	19-19-15	21-19-15	23-19-15	19-19-15	21-19-15	19-19-15
VS	150+2	151+2	150+3	150+2	158+3	157+2
SC	67, paired	68, paired	67, paired	67, paired	57, paired	64, paired
VS+SC	217	219	217	217	215	221
CP	1	1	1	1	1	1
Eye color	Amber with a faint reddish hue	Amber with a faint reddish hue	Amber	Amber	Yellowish	Yellowish
Postocular streak	Thin and white, with a few scale margins tinged with yellow	White	Thin and white, with the upper margins of a few scales tinged with reddish-brown	Thin and white, with a few scale margins tinged with yellow	Absent	Absent
Ventrolateral stripe	Yellow+white+red+brown	Thin, white and tinged with yellowish margins	Yellow+white+red+brown	Yellow+white+red+brown	White	Absent

while only limited information is available for females due to the small sample size. This species exhibits sexual dichromatism. In males, the eyes are amber in color. Among the two adult specimens (QHU R2025027 and QHU R2025028), the irises exhibit a slight reddish hue, whereas in the two subadult specimens (QHU R2025029 and QHU R2025030), the eyes are purely amber. The postocular streak is narrow and white, with a few scale margins slightly tinged with yellow or reddish-brown. The ventrolateral stripe runs along the first dorsal scale row and is variable in coloration among males, occurring in two forms. In most male specimens, it consists of a narrow white band bordered dorsally by a faint yellowish margin and ventrally by a thin, red line, with a diffuse brownish tinge below the red line. However, in QHU R2025028, the ventrolateral stripe is only a narrow white band bordered on both sides by faint yellowish margins. In some individuals, the upper and lower margins of the first dorsal scale row remain green.

In females, the eyes are yellowish. The postocular streak is absent in both specimens. The ventrolateral stripe is absent in QHU R2025032, while in QHU R2025031 it is narrow, white, and restricted to the middle portion of the first dorsal scale row.

In all individuals, the dorsal surfaces of the head and body are grass green. In males, the lateral body coloration

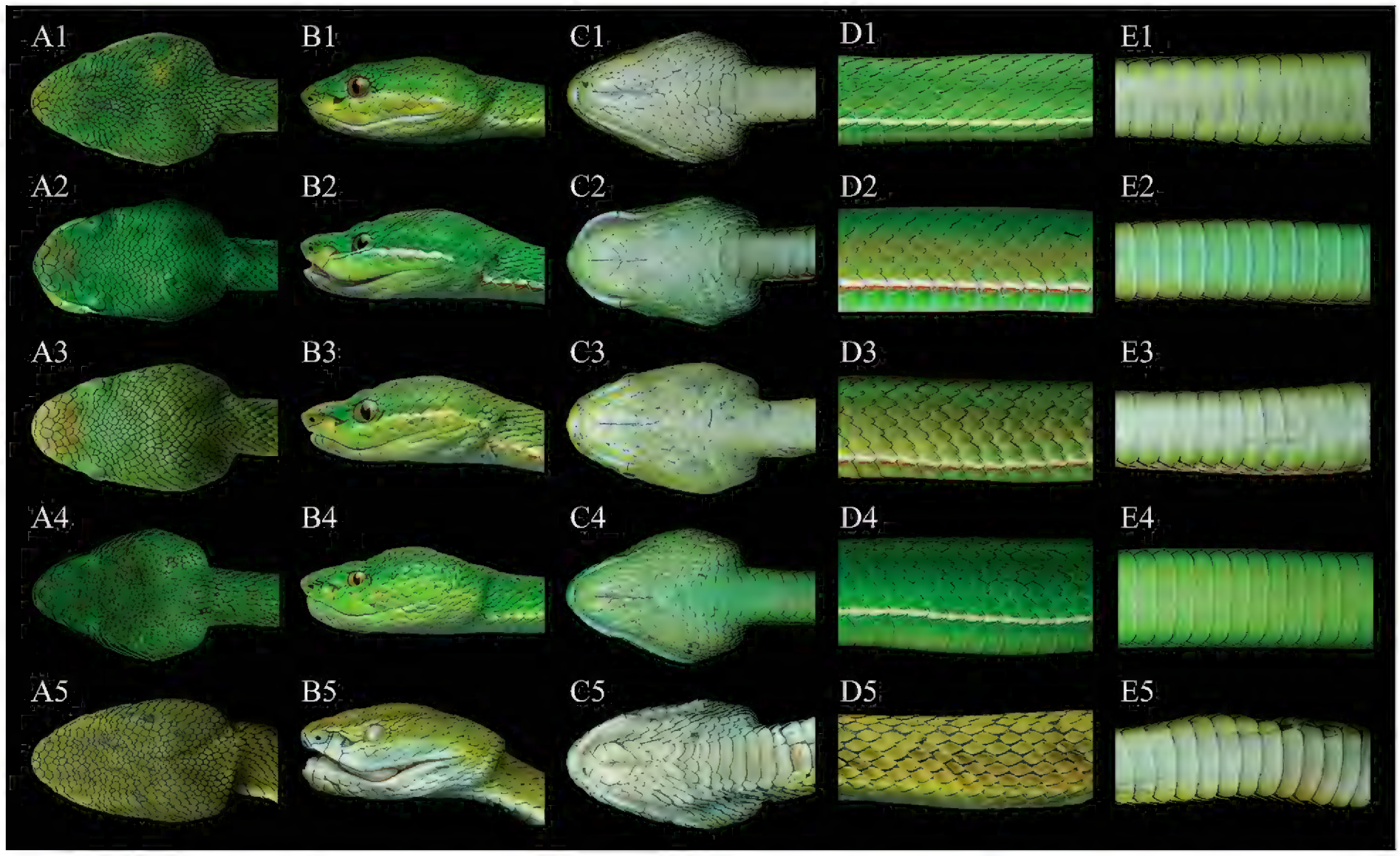

Figure 7. Paratypes of *Trimeresurus loong* sp. nov. **A.** Dorsal view of the head; **B.** Lateral view of the head; **C.** Ventral view of the head; **D.** Lateral view of the body; **E.** Ventral view of the body. **A1–E1.** QHU R2025028, adult male; **A2–E2.** QHU R2025029, subadult male; **A3–E3.** QHU R2025030, subadult male; **A4–E4.** QHU R2025031, adult female; **A5–E5.** QHU R2025032, adult female. Photographs by Y.H. Xu.

is slightly paler than the mid-dorsal region, and the lateral dorsal scales are variably speckled with fine creamish-blue or white spots. In contrast, females exhibit a uniformly grass-green coloration across the entire dorsum. The dorsal surface of the tail is distinctly bicolored: green anteriorly, gradually transitioning to nearly uniform orange or light orange-red posteriorly, with the tail tip being blackish brown (Fig. 6B–E). The ventral surface of the head and the central portion of the anterior ventral body are noticeably paler, appearing pale whitish-green or creamish-yellow. Posterior to midbody, the ventral coloration becomes uniformly yellowish-green or light green. The anterior portion of ventral surface of the tail is pale green, while the posterior portion is light orange-red.

Main characters of the pattern in preservative. The description is based on a subadult male specimen (QHU R2025029) and a female specimen (QHU R2025032), both collected in May 2025. After approximately five months in alcohol, the dorsal surface of the head had turned olive-yellow and that of the body yellow in both specimens. The eyes had become pale gray, and the supralabials as well as the ventral surface of the head had faded to milky white. The lateral portions of the ventral body were pale yellow, while the entire central ventral surface had turned creamish-yellow. In the male specimen, the posterior portion of the ventral body was slightly yellowish-green. The orange-red area of the tail remained relatively well defined. In the male specimen, the ventrolateral stripe had changed to white dorsally and brownish with a slight reddish hue ventrally.

Distribution and natural history. Currently, *Trimeresurus loong* sp. nov. is certainly known only from the type locality, Qinglongxia, Anning City, Kunming City, Yunnan Province, China, at an elevation of approximately 1,822 m asl. All specimens were encountered during the first half of the night, coiled within shrubs on hillsides near streams in well-preserved broad-leaved forest (Fig. 10A–C), when nighttime temperatures ranged 15 °C ~ 18 °C. The female specimen QHU R2025031 defecated immediately when disturbed during capture. Its feces contained numerous bird feathers, suggesting that small birds may constitute part of the adult diet of this species (Fig. 10D).

Comparisons. *Trimeresurus loong* sp. nov. is assigned to the subgenus *Viridovipera* based on a combination of diagnostic characters, including its phylogenetic position, the complete separation of the first supralabial from the nasal scale, and a short spinose hemipenis, all of which are characteristic features of *Viridovipera* (e.g., Nguyen et al. 2025; Xu et al. 2025). Accordingly, morphological comparisons are restricted to congeners within *Viridovipera*, which currently comprises nine recognized species and represents the most relevant group for differential diagnosis. The principal characters distinguishing *Trimeresurus loong* sp. nov. from these congeners are summarized in Table 5 and illustrated in Fig. 10.

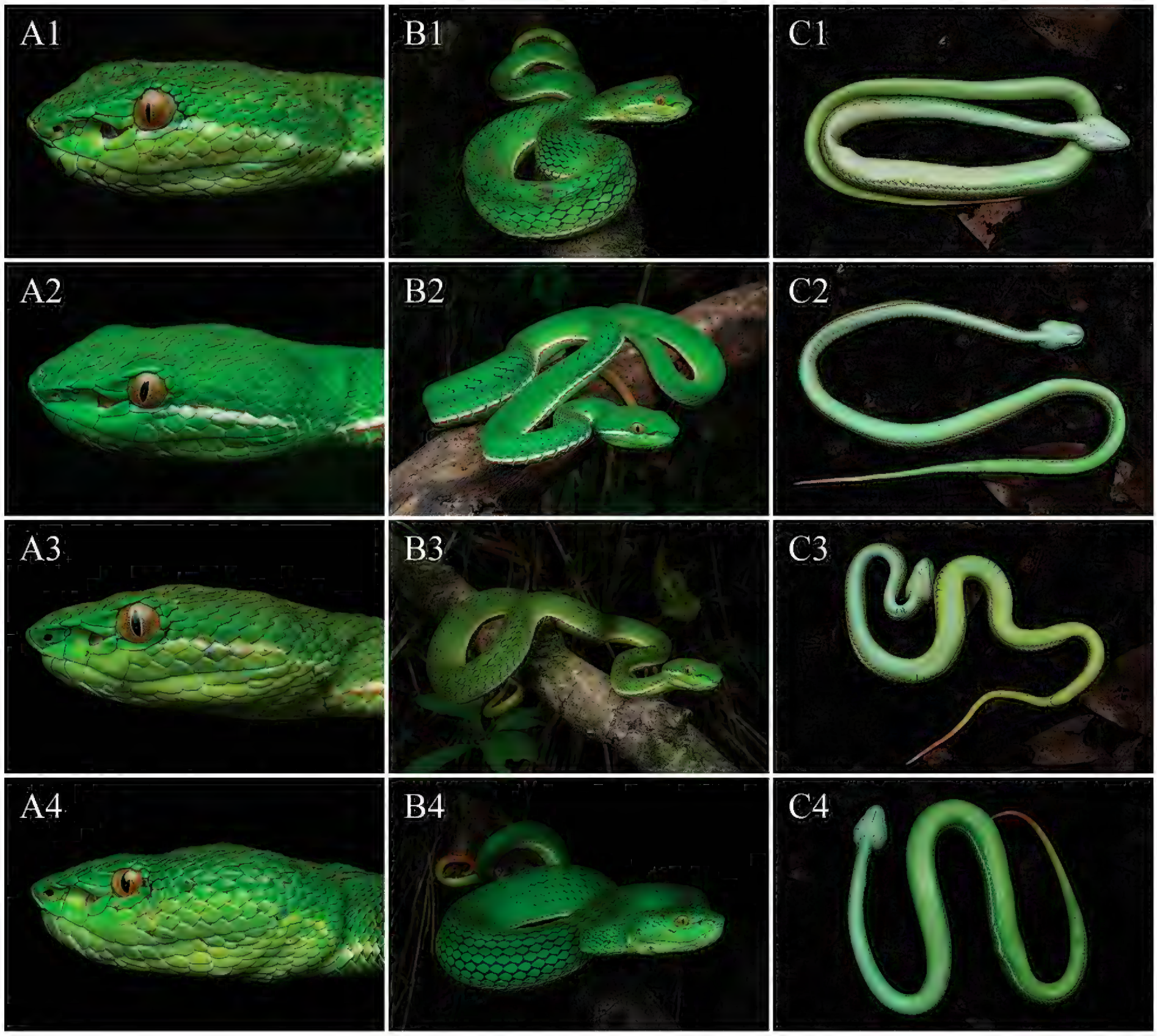

Figure 8. Coloration of the paratypes of *Trimeresurus loong* sp. nov. in life. **A.** Lateral view of the head; **B.** Dorsolateral view; **C.** Ventral view. **A1–C1.** QHU R2025028, adult male; **A2–C2.** QHU R2025029, subadult male; **A3–C3.** QHU R2025030, subadult male; **A4–C4.** QHU R2025031, adult female. Photographs by Y.H. Xu.

Morphologically, *Trimeresurus loong* sp. nov. is most similar to *T. yunnanensis* (distributed in central to southwestern Yunnan Province of China, the Mandalay Region and Shan State of Myanmar, northern Laos, northern and central Thailand, and northern to central Vietnam), but it can be clearly distinguished from the latter by the following combination of characters: (1) smaller maximum SVL in females (657 mm vs. 804 mm); (2) lower total number of VS+SC in males (217–219 [mean 217.5 ± 1.0] vs. 221–231 [mean 225.9 ± 3.9]); (3) irises amber in males vs. bright or deep red irises observed in males of *T. yunnanensis* (Fig. 10A, B, K); (4) the ventrolateral stripe in the males of the new species is slender and limited to the first dorsal scale row occurring in two forms, either a narrow white band bordered dorsally by a faint yellowish margin and ventrally by a red line with a diffuse brownish tinge below the red line, or a narrow white band bordered by faint yellowish margins on both sides, while in the males of *T. yunnanensis* the stripe is broader and more vivid, occupying the entire first dorsal scale row and the lower margin of the second row, even extending onto the lateral edges of the ventrals, consisting of a thick red lower border and a white upper zone with sharply separated colors visible from a distance; (5) the new species has a anteriorly green coloration of tail, posteriorly gradually transitioning to a uniformly orange or light orange-red. In contrast, *T. yunnanensis* shows dark red blotches forming large, irregular patches with uneven margins on the anterior part of the tail (Fig. 11). In hemipenial morphology, *Trimeresurus loong* sp. nov. can be distinguished from *T. yunnanensis* by shorter hemipenial truncus and a higher degree of bifurcation (HCL/HTL ratio 0.62–0.66 vs. 0.69), a more distal sulcus spermaticus bifurcation point (SPBD/HCL ratio 0.43–0.49 vs. 0.30), and a greater number of enlarged spines (14–19 per side vs. 9–10, excluding the smaller spines lining the margin of the sulcus spermaticus) (Fig. 4A, B, F).

Figure 9. Habitat and field observations of *Trimeresurus loong* sp. nov. **A.** The microhabitat of the new species in Anning, Kunming, China; **B.** Holotype QHU R2025027 in life, in situ; **C.** Paratype QHU R2025028 in life, in situ; **D.** Feces of the paratype QHU R2025031. Photographs by Y.H. Xu (**A–C**) and J.D. Deng (**D**).

Trimeresurus loong sp. nov. differs from *T. mayaae* (distributed across the Indian States of Manipur, Meghalaya, Mizoram, Assam, Nagaland, West Bengal, Sikkim, Bhutan, and Chin State of Myanmar) by the following combination of characters: larger maximum SVL in females (657 mm vs. 590 mm); lower number of VS in males (150–151 [mean 150.3 ± 0.5] vs. 153–163 [mean 158.1 ± 3.0]); higher number of SC in females (57–64 [mean 60.5 ± 4.9] vs. 53–55 [mean 54.0 ± 1.0]); and higher number of VS+SC in females (215–221 [mean 218.0 ± 4.2] vs. 205–208 [mean 206.7 ± 1.5]). In addition, females of *Trimeresurus loong* sp. nov. have yellowish irises, distinctly differing from the greenish eyes of *T. mayaae*.

Trimeresurus loong sp. nov. differs from *T. medoensis* (distributed in the Xizang AR of southwestern China, and possibly in northern Myanmar and northeastern India) by the following combination of characters: slight larger maximum SVL in both sexes (601 mm in males, 657 mm in females vs. 553 mm in males, 624 mm in females); higher number of VS in both sexes (150–151 [mean 150.3 ± 0.5] in males, 157–158 [mean 157.5 ± 0.7] in females vs. 146–151 [mean 148.6 ± 1.8] in males, 145–147 [mean 146.0 ± 1.0] in females); greater number of SC in males (67–68 [mean 67.3 ± 0.5] vs. 55–59 [mean 57.0 ± 1.4]); and higher number of VS+SC in both sexes (217–219 [mean 217.5 ± 1.0] in males, 215–221 [mean 218.0 ± 4.2] in females vs. 201–208 [mean 205.6 ± 2.9] in males, 204–206 [mean 205.0 ± 1.0] in females). The new species also possesses a greater number of SL (10–11 vs. 8–9) and IL (11–14 vs. 8–10). It further differs in having more dorsal scale rows at midbody (19 vs. 17) and posteriorly (15 vs. 13, rarely 11). Eye coloration also differs: males of new species have amber irises with a slight reddish hue, and females yellowish, whereas both sexes of *T. medoensis* possess green or yellowish-green eyes (Fig. 10A, B, E). In addition, the ventrolateral stripe in females of new species is absent or uniformly white, contrasting with the red-and-white stripe of *T. medoensis*. In hemipenial morphology, *Trimeresurus loong* sp. nov. can be distinguished from *T. medoensis* by longer hemipenial truncus and a lower degree of bifurcation (HCL/HTL ratio 0.62–0.66 vs. 0.53), and a more distal sulcus spermaticus bifurcation point (SPBD/HCL ratio 0.43–0.49 vs. 0.21) (Fig. 4A–C).

Trimeresurus loong sp. nov. differs from *T. nujiang* (distributed across several localities within the Nujiang River Basin of northwestern Yunnan Province, China, including Gongshan, Fugong, and Lushui Conties) by the following combination of characters: slightly smaller maximum SVL in both sexes (601 mm in males, 657 mm in females vs. 694 mm in males, 682 mm in females); lower number of

Table 5. Summary of morphological characters in members of the subgenus *Viridovipera*. Notes: Diagnostic characters distinguishing *Trimeresurus loong* sp. nov. are indicated in bold.

Trimeresurus	**Sources**	**Max SVL (mm)**		**VS**		**SC**		**VS+SC**		**ASR**	**MSR**	**PSR**	**SL**	**IL**
		♂	♀	♂	♀	♂	♀	♂	♀					
T. loong sp. nov.	(19)	601	657	150–151 [150.3 ± 0.5]	157–158 [157.5 ± 0.7]	67–68 [67.3 ± 0.5]	57–64 [60.5 ± 4.9]	217–219 [217.5 ± 1.0]	215–221 [218.0 ± 4.2]	19–23	19	15	10 or 11	11–14
T. mayaae	(7), (8), (9), (14), (15), (16)	610	**590**	**153–163 [158.1 ± 3.0]**	**152–153 [152.7 ± 0.6]**	54–69 [61.1 ± 4.5]	**53–55 [54.0 ± 1.0]**	211–231 [218.9 ± 6.1]	**205–208 [206.7 ± 1.5]**	19–28	19–21	15–17	8–10	10–13
T. medoensis	(4), (13), (16)	**553**	**624**	**146–151 [148.6 ± 1.8]**	**145–147 [146.0 ± 1.0]**	**55–59 [57.0 ± 1.4]**	58–60 [59.0 ± 1.0]	**201–208 [205.6 ± 2.9]**	**204–206 [205.0 ± 1.0]**	**17 (rarely 19)**	**17**	**13 (rarely 11)**	**8 or 9**	**8–10**
T. nujiang	(17)	**694**	**682**	**164–173 [168.7 ± 3.6]**	**165–168 [166.6 ± 1.3]**	59–68 [62.8 ± 3.9]	57–60 [58.2 ± 1.1]	**226–241 [231.3 ± 6.8]**	**222–226 [224.8 ± 1.8]**	19–21 (rarely 22)	19	15	9 or 10	11–13
T. pretiosus	(18)	**516**	**512**	**140–143 [141.5 ± 2.1]**	**142**	**56–58 [57.0 ± 1.4]**	**54**	**198–199 [198.5 ± 0.7]**	**196**	19	19	15	**8 or 9**	10 or 11
T. stejnegeri	(1), (3), (16)	635	670	**154–178 [164.5 ± 4.8]**	155–173 [163.9 ± 3.5]	60–80 [70.3 ± 4.2]	58–70 [63.4 ± 2.9]	**218–256 [234.9 ± 7.7]**	218–237 [227.5 ± 4.5]	21–25	**21–23**	15	9–12	10–14
T. truongsonensis	(8), (11), (16)	**521**	**488**	**170–190 [179.8 ± 8.7]**	**165–167 [166.0 ± 1.0]**	65–71 [67.4 ± 2.5]	61–70 [66.7 ± 4.9]	**235–259 [247.2 ± 10.7]**	**228–235 [232.7 ± 4.0]**	21	**21**	15	9–11	11–13
T. vogeli	(5), (16)	**661**	**947**	**157–169 [162.8 ± 3.7]**	157–173 [164.2 ± 5.8]	63–71 [67.0 ± 2.3]	59–70 [63.0 ± 3.8]	**221–238 [229.8 ± 4.9]**	218–238 [227.7 ± 6.3]	21–23	**21 (rarely 20)**	15	9–11	11–16
T. yunnanensis	(2), (3), (6), (10), (12), (17)	602	**804**	151–164 [158.2 ± 3.9]	150–164 [157.9 ± 3.6]	61–71 [66.1 ± 2.9]	52–65 [57.8 ± 3.6]	**221–231 [225.9 ± 3.9]**	211–223 [216.4 ± 3.7]	19–21	19–21	15–17	9–11	10–13

Trimeresurus	**Eye color in life**		**Postocular streak in life**		**Ventrolateral stripe in life**		**Tail red**	**Tail red pattern**	**Body colouration in life**
	♂	♀	♂	♀	♂	♀			
T. loong sp. nov.	amber, sometimes with a slight reddish hue	yellowish	thin and white, with a few scale margins slightly tinged with yellow or reddish-brown	absent	yellow + white + red + brown or thin, white with yellowish margins	absent or white, thin	yes	orange or light orange-red, uniform, blackish brown at the tip	uniformly grass-green
T. mayaae	**rusty or greenish**	**greenish**	none or red + white	absent	**red + white, wide**	pale yellow + white, thin	yes	**rusty red, forming blotches anteriorly**	uniformly grass-green
T. medoensis	**green or yellowish green**	**green or yellowish green**	none or faint white	absent	**red + white, wide**	**red + white**	yes	**red to dark rusty red, sometimes forming blotches anteriorly**	uniformly grass-green
T. nujiang	**golden yellow**	golden yellow	**none**	absent	**dark red + white**	faint white	yes	**reddish-brown with dark brown at the tip**	uniformly grass-green
T. pretiosus	**reddish-brown**	orange-yellow	none or very faint, thin white	absent	**red + white, wide**	white, thin	yes	**brick-red, sometimes forming blotches anteriorly**	uniformly grass-green
T. stejnegeri	bright red or orange-red (rarely yellow)	yellow or orange	red + white or white	absent or white, thin	**red + white, wide**	red + white or white	yes	light orange-red to red, uniform or forming blotches anteriorly	uniformly grass-green
T. truongsonensis	**greenish-yellow**	**greenish-yellow**	**none**	absent	**red + brown, wide**	**red + brown**	**no**	**–**	**greenish blue with brown broad bands**
T. vogeli	**light orange**	**light orange**	none or faint white	absent	**red + white, wide**	**pale yellow + white, thin**	**no**	**–**	uniformly grass-green
T. yunnanensis	**bright or deep red**	golden yellow	red + white or white or absent	absent or white, thin	**red + white, wide**	absent or white or pale green, thin	yes	**dark red, with large anterior blotches and irregularly shaped margins**	uniformly grass-green

Sources: (1) = Maki 1931; (2) = Pope 1935; (3) = Zhao et al. 1998; (4) = David et al. 2001a; (5) = David et al. 2001b; (6) = David et al. 2002; (7) = Ao et al. 2004; (8) = Orlov et al. 2004; (9) = David and Mathew 2005; (10) = Guo et al. 2009; (11) = Teynié and David 2004; (12) = Nguyen et al. 2018; (13) = Che et al. 2020; (14) = Rathee et al. 2022; (15) = Elangbam et al. 2023; (16) = Nguyen et al. 2025; (17) = Liang et al. 2025; (18) = Xu et al. 2025; (19) = this study.

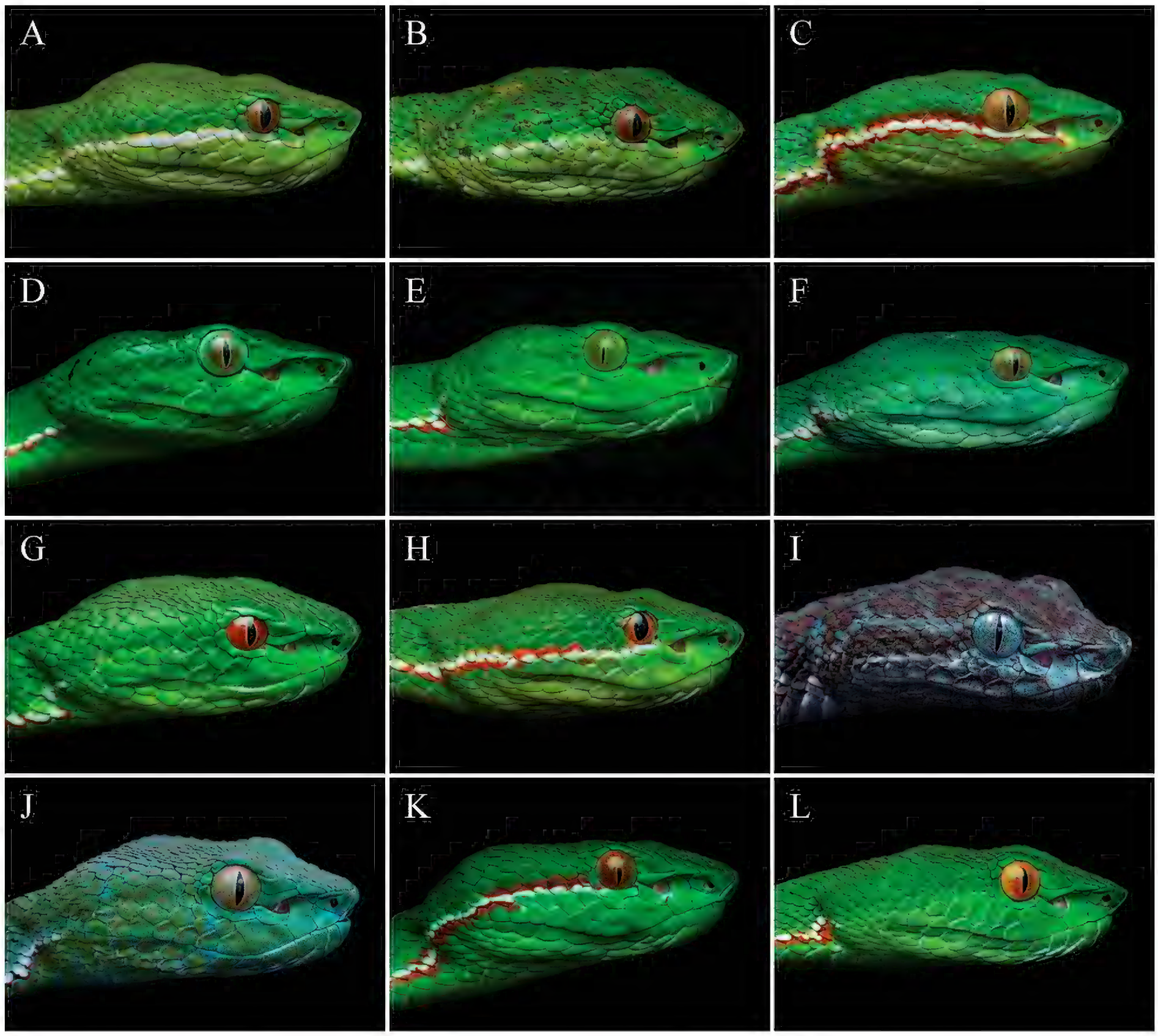

Figure 10. Comparison of the lateral head view of males of species in the subgenus *Viridovipera* in life. **A.** *Trimeresurus loong* sp. nov., QHU R2025027, holotype; **B.** *Trimeresurus loong* sp. nov., QHU R2025028, paratype; **C.** *Trimeresurus* sp. from Chengdu, Sichuan, China; **D.** *T. mayaae* from Kangpokpi, Manipur, India; **E.** *T. medoensis*, QHU R2025040, from Motuo (Medog), Xizang, China; **F.** *T. nujiang* from Gongshan, Yunnan, China; **G.** *T. pretiosus*, QHU R2025020, from Yadong, Xizang AR, China; **H.** *T. stejnegeri*, QHU R2025037, from Lishui, Zhejiang, China; **I.** *T. truongsonensis* from Phong Nha-Ke Bang NP, Quang Tri, Vietnam; **J.** *T. vogeli* from Phong Nha-Ke Bang NP, Quang Tri, Vietnam; **K.** *T. yunnanensis* from Jingdong, Yunnan, China; **L.** *T.* cf. *yunnanensis* from Mt. Dawei, Honghe, Yunnan, China. Photographs by Y.H. Xu (**A–C**, **E–L**) and P. Shinde (**D**).

VS in both sexes (150–151 [mean 150.3 ± 0.5] in males, 157–158 [mean 157.5 ± 0.7] in females vs. 164–173 [mean 168.7 ± 3.6] in males, 165–168 [mean 166.6 ± 1.3] in females); and lower number of VS+SC in both sexes (217–219 [mean 217.5 ± 1.0] in males, 215–221 [mean 218.0 ± 4.2] in females vs. 226–241 [mean 231.3 ± 6.8] in males, 222–226 [mean 224.8 ± 1.8] in females). Eye coloration also differs, with males of the new species having amber irises with a slight reddish hue vs. yellow or mottled gray and flesh-colored in *T. nujiang* (Fig. 10A, B, F). In addition, a postocular streak is present in males of new species but absent or very faint in *T. nujiang*.

Trimeresurus loong sp. nov. differs from *T. pretiosus* (distributed in Yadong County, Xigaze City, Xizang AR, China) by the following combination of characters: having a larger maximum SVL in both sexes (601 mm in males, 657 mm in females vs. 516 mm in males, 512 mm in females); a higher number of VS (150–151 [mean 150.3 ± 0.5] in males, 157–158 [mean 157.5 ± 0.7] in females vs. 140–143 [mean 141.5 ± 2.1] in males, 142 in female); a greater number of SC (67–68 [mean 67.3 ± 0.5] in males, 57–64 [mean 60.5 ± 4.9] in females vs. 56–58 [mean 57.0 ± 1.4] in males, 54 in female); a higher number of VS+SC (217–219 [mean 217.5 ± 1.0] in males, 215–221 [mean 218.0 ± 4.2] in females vs. 198–199 [mean 198.5 ± 0.7] in males, 196 in female); a greater number of supralabials (10 or 11 vs. 8 or 9); in possessing all subcaudal scales paired (vs. partly single); and eye coloration in males is

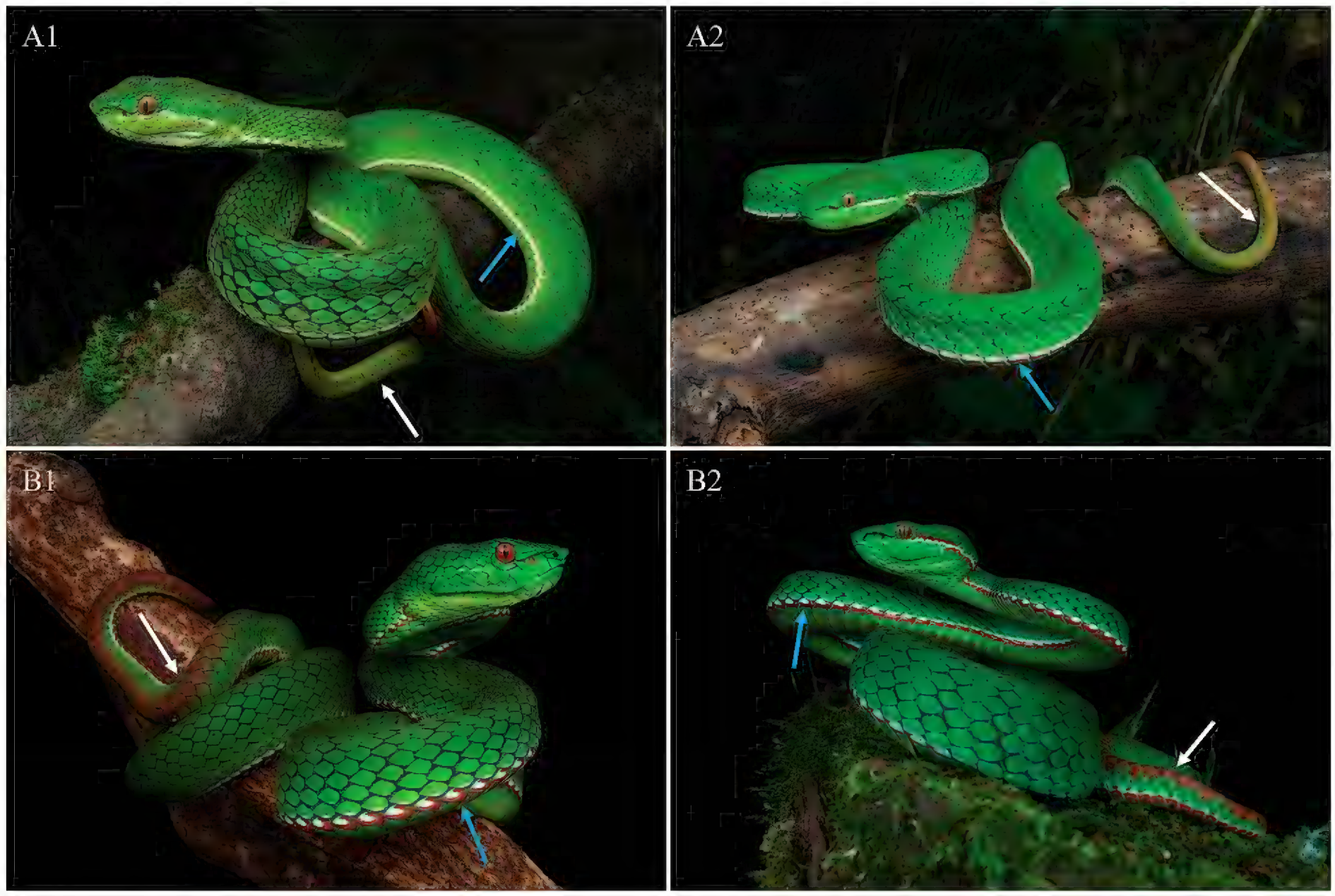

Figure 11. Comparison of male coloration between *Trimeresurus loong* sp. nov. and *T. yunnanensis*. **A1.** *Trimeresurus loong* sp. nov., QHU R2025028; **A2.** *Trimeresurus loong* sp. nov., QHU R2025029; **B1.** *T. yunnanensis*, QHU R2025035, from Lincang, Yunnan, China; **B2.** *T. yunnanensis*, unvouchered individual from Jingdong, Yunnan, China. The white arrows indicate the dorsal surface of the tail, and blue arrows indicate the ventrolateral stripe. Photographs by Y.H. Xu.

amber with a slight reddish hue (vs. brick red) (Fig. 10A, B, G). In hemipenial morphology, *Trimeresurus loong* sp. nov. can be distinguished from *T. pretiosus* by longer hemipenial truncus and a lower degree of bifurcation (HCL/HTL ratio 0.62–0.66 vs. 0.47–0.53), and a more distal sulcus spermaticus bifurcation point (SPBD/HCL ratio 0.43–0.49 vs. 0.28–0.36) (Fig. 4A, B, D).

Trimeresurus loong sp. nov. differs from *T. stejnegeri* (restricted to eastern and southern China, including Taiwan Province, northern Vietnam, and northeastern Laos) by the following combination of characters: lower VS in males (150–151 [mean 150.3 ± 0.5] vs. 154–178 [mean 164.5 ± 4.8]); lower number of VS+SC in males (217–219 [mean 217.5 ± 1.0] vs. 218–256 [mean 234.9 ± 7.7]); and fewer dorsal scale rows at midbody (19 vs. 21–23). In males, the irises are amber with a slight reddish hue, and the ventrolateral stripe is slender and confined to the first dorsal scale row, occurring in two forms: either a narrow white band bordered dorsally by a faint yellowish margin and ventrally by a red line with a diffuse brownish tinge below the red line, or a narrow white band bordered by faint yellowish margins on both sides in *Trimeresurus loong* sp. nov. In contrast, in *T. stejnegeri*, the irises are orange-red or red (Fig. 10A, B, H), and the ventrolateral stripe consists of a red lower border and a white upper zone, with the two colors sharply separated and clearly visible from a distance. In females, the ventrolateral stripe is uniformly white, whereas in *T. stejnegeri* it is white or red-and-white. In hemipenial morphology, *Trimeresurus loong* sp. nov. can be distinguished from *T. stejnegeri* by shorter hemipenial truncus and a higher degree of bifurcation (HCL/HTL ratio 0.62–0.66 vs. 0.69), and a more distal sulcus spermaticus bifurcation point (SPBD/HCL ratio 0.43–0.49 vs. 0.28) (Fig. 4A, B, E).

Trimeresurus loong sp. nov. differs from *T. truongsonensis* (restricted to central Vietnam and central Laos) by the following combination of characters: a larger maximum SVL in both sexes (601 mm in males, 657 mm in females vs. 521 mm in males, 488 mm in females); a lower number VS (150–151 [mean 150.3 ± 0.5] in males, 157–158 [mean 157.5 ± 0.7] in females vs. 170–190 [mean 179.8 ± 8.7] in males, 165–167 [mean 166.0 ± 1.0] in females); a greater number of SC (67–68 [mean 67.3 ± 0.5] in males, 57–64 [mean 60.5 ± 4.9] in females vs. 56–58 [mean 57.0 ± 1.4] in males, 54 in the female); and consequently a lower number of VS+SC (217–219 [mean 217.5 ± 1.0] in males, 215–221 [mean 218.0 ± 4.2] in females vs. 235–259 [mean 247.2 ± 10.7] in males, 228–235 [mean 232.7 ± 4.0] in females); and fewer dorsal scale rows at midbody (MSR 19 vs. 21). Eye coloration is amber with a slight reddish hue in males and yellowish in females, contrasting with the greenish-yellow eyes of both sexes in

the latter species (Fig. 10A, B, I). The body is uniformly bright grass-green, whereas *T. truongsonensis* exhibits a greenish-blue dorsum with broad brown crossbands.

Finally, *Trimeresurus loong* sp. nov. differs from *T. vogeli* (distributed in the southeastern part of central Thailand, central and southern Laos, Cambodia, and central and southern Vietnam) by the following combination of characters: smaller maximum SVL in both sexes (601 mm in males, 657 mm in females vs. 661 mm in males, 947 mm in females); lower number of VS in males (150–151 [mean 150.3 ± 0.5] vs. 157–169 [mean 162.8 ± 3.7]); lower number of VS+SC in males (217–219 [mean 217.5 ± 1.0] vs. 221–238 [mean 229.8 ± 4.9]); fewer dorsal scale rows at midbody (MSR 19 vs. 21, rarely 20); and eye coloration in males is amber with a slight reddish hue (vs. light orange or flesh-colored) (Fig. 10A, B, J).

Discussion

Pholidosis (i.e., the pattern and arrangement of scales) has long been considered one of the most important diagnostic features for species identification and classification in snakes. However, in the genus *Trimeresurus*, scale counts are often highly conserved, making taxonomic delimitation particularly challenging (Guo et al. 2009; David et al. 2011; Sumontha et al. 2021; Idiiatullina et al. 2024b; Nguyen et al. 2025; Pawangkhanant et al. 2025). Many closely related species are nearly indistinguishable based on scalation characters alone, especially within the subgenus *Viridovipera*, where several taxonomic units had long been misidentified as *T. stejnegeri* or *T. yunnanensis* (Schmidt 1927; Pope 1935; Smith 1943; Zhao et al. 1998; Creer et al. 2003; Malhotra and Thorpe 2004a, b; Zhao 2006; Guo et al. 2009; Rathee et al. 2022; Wu et al. 2023; Liang et al. 2025). For example, *T. mayaae*, *T. nujiang*, and the newly described *Trimeresurus loong* sp. nov. were previously regarded as geographically distinct populations of *T. yunnanensis* (Zhao et al. 1998; Malhotra and Thorpe 2004a, b; Zhao 2006; Rathee et al. 2022; Wu et al. 2023; Liang et al. 2025). In recent years, the incorporation of molecular phylogenetic data has gradually uncovered the true diversity within *Viridovipera*, revealing that this subgenus harbors a greater number of cryptic species than previously recognized. Nonetheless, due to significant overlap in pholidosis among many taxa, the inclusion of more diverse morphological characters is essential for accurate species identification and classification. One such promising character set is coloration pattern, which has shown potential in resolving taxonomic ambiguities in this group. Sexual dichromatism is common in *Viridovipera*, with males typically exhibiting more vivid and distinctive coloration patterns that are often stable within species. As such, comparisons of male coloration traits can provide important diagnostic clues for species delimitation. Three recently described species, *T. mayaae*, *T. pretiosus*, and *T. nujiang* in *Viridovipera* have also employed coloration features as key diagnostic characters (Rathee et al. 2022; Liang et al. 2025; Xu et al. 2025). *Trimeresurus loong* sp. nov. is likewise distinguished by its unique coloration traits. Although it was once misidentified as *T. yunnanensis*, the two species can be readily distinguished in males by differences in eye coloration, as well as in the color pattern of the ventrolateral stripe and dorsal tail.

In addition, hemipenial morphology serves as another effective diagnostic feature. Although the hemipenes of *Viridovipera* species have been described in previous studies (Pope 1935; Malhotra and Thorpe 2004a; Orlov et al. 2004; Dawson et al. 2008; Guo et al. 2009; Rathee et al. 2022; Liang et al. 2025; Xu et al. 2025), most accounts were based on incompletely everted or poorly preserved specimens, thereby limiting their diagnostic value. A comprehensive interspecific comparison has remained lacking. In this study, we compared the hemipenes of five species (Fig. 4) within the subgenus *Viridovipera* and found that the primary differences involve the degree of bifurcation, the relative position of the sulcus spermaticus bifurcation point, and the number of enlarged spines. While Guo et al. (2009) described variation in the zonation of the spine and calyx regions among several species, our results indicate that these features are, in fact, remarkably similar across taxa. The previously reported discrepancies may result from methodological differences in hemipenis preparation, including the use of inflation materials and preservation state, which can distort the apparent shape (Myers and Cadle 2003). Moving forward, hemipenial morphology should be documented across a broader range of species within *Viridovipera*, and the terminology and preparation techniques should be standardized to ensure consistent taxonomic interpretations. Taken together, both morphological and molecular evidence consistently support the distinctiveness of *Trimeresurus loong* sp. nov. within *Viridovipera*.

The new species *Trimeresurus loong* sp. nov. represents a distinct evolutionary lineage within the subgenus *Viridovipera*. Phylogenetic analyses based on mitochondrial DNA (*16S*, cyt *b*, and *ND4* genes) recovered *T. loong* sp. nov. as sister to *T.* cf. *loong* from Huili City, Sichuan Province, China, with moderate statistical support (SH = 83; UFB = 92; PP = 0.97). Together, they form a clade with an unidentified *Trimeresurus* lineage from western Sichuan Province, China. This entire assemblage occupies a peripheral position relative to the remaining recognized species of *Viridovipera*, and *Trimeresurus loong* sp. nov. exhibits substantial genetic divergence from all currently recognized congeners, with uncorrected *p*-distances of at least 6.7% (cyt *b*) and 6.1% (*ND4*). This level of divergence, combined with consistent morphological differentiation, supports its recognition as a valid species. Moreover, the specimens previously recorded as *T. yunnanensis* by Schmidt (1927) and Pope (1935) from "Yunnan-fu" (now Kunming City, Yunnan Province; specimen MCZ 14671, a paratype of *T. yunnanensis*), those listed by Zhao et al. (1998) from Kunming (specimens KIZ 72001, KIZ 73008, and KIZ 85702), as well as specimen NHMUK 1904.11.29.29 from "Yunnan-fu" housed at the Natural History Museum, London, may likewise represent *Trimeresurus loong* sp. nov. (Table 6). However, due to the

Table 6. Specimens from Kunming, Yunnan, China previously assigned to *Trimeresurus yunnanensis*. Remark: N/a = not available.

Collection number	Sex	SVL (mm)	TAL (mm)	ASR	MSR	PSR	VS	SC	SL	IL	Source
KIZ 72001	♂	417	100	20	19	15	157	71	9/10	11/11	Zhao et al. (1998)
KIZ 73008	♀	457	99	19	19	15	150	57	10/11	12/11	Zhao et al. (1998)
KIZ 85702	♀	617	141	21	19	15	158	65	10/10	11/11	Zhao et al. (1998)
MCZ 14671	♂	N/a	N/a	21	19	15	160	68	N/a	N/a	Schmidt (1927); Pope (1935)
NHMUK 1904.11.29.29	♀	652	137	21	20	15	156	55	10/10	12/12	This study

lack of direct examination, the coloration of these specimens from Kunming City and its surrounding areas remains uncertain. Further reassessment is therefore necessary to determine whether they indeed represent *Trimeresurus loong* sp. nov., or whether the two species exhibit partially overlapping distributions.

Liang et al. (2025) recently synonymized *T. gumprechti* with *T. yunnanensis* on the basis of minimal genetic divergence and overlapping morphological variation. Nevertheless, some specimens included in their comparative dataset appear to have been assigned to different taxa. For instance, ZFMK 92790 and ZFMK 92791 from Phuoc Binh National Park, Ninh Thuan Province (currently Khanh Hoa Province), southern Vietnam, were labeled as *T. gumprechti* but seem morphologically consistent with *T. vogeli* (T.V. Nguyen, pers. obs.). Likewise, CAS 241182 from Moenyin Township, Myitkyina District, Kachin State, northern Myanmar, appears referable to *T. popeiorum* (see Idiiatullina et al. 2024b), and ZFMK 92793 from Chu Yang Sin National Park, Dak Lak Province, southern Vietnam, initially identified as *T. stejnegeri*, also corresponds to *T. vogeli*. Such errors may have affected their taxonomic interpretation and highlight the need for a thorough re-examination of comparative material used in their study. Considering the recent descriptions of *T. nujiang* and *T. pretiosus*, it is evident that southwestern China harbors multiple cryptic lineages of the subgenus *Viridovipera* with restricted distributions. The discovery of *Trimeresurus loong* sp. nov. from Kunming City, Yunnan Province, further supports the view that *T. yunnanensis* sensu lato represents a complex of closely related species that warrants comprehensive revision using both genomic and morphological data. The discovery of *Trimeresurus loong* sp. nov. underscores the taxonomic complexity of the *T. yunnanensis* group and the importance of integrative approaches in resolving cryptic diversity among Asian green pit vipers.

Biogeographically, the occurrence of *Trimeresurus loong* sp. nov. in the Anning City, Kunming City adds an important element to our understanding of *Viridovipera* diversification in Yunnan Province. This area represents a transitional zone between the Red River drainage and the Yunnan-Guizhou Plateau, characterized by dissected montane terrain and broad-leaved forests or coniferous forests. The restricted range of *Trimeresurus loong* sp. nov. contrasts with the more westernly species *T. nujiang* and the Himalayan occurrence of *T. pretiosus*. Together, these species reveal a clear geographic and elevational gradient of diversification within the *Viridovipera*, likely influenced by complex orogeny, climatic oscillations, and ecological isolation. The narrow ventrolateral stripe, light orange red tail, and amber iris of *Trimeresurus loong* sp. nov. may represent local adaptive features associated with its mid-montane forest environment. With the discovery of *Trimeresurus loong* sp. nov., the total number of *Trimeresurus* species recorded from Yunnan Province now rises to nine, including two species endemic to Yunnan, namely *Trimeresurus loong* sp. nov. and *T. nujiang*. These endemics further emphasize Yunnan's exceptional biogeographic heterogeneity and its role as a core diversification center for Asian green pit vipers.

From a conservation perspective, *Trimeresurus loong* sp. nov. is currently known only from its type locality in Qinglongxia, Anning City, Kunming City, Yunnan Province, China, at an elevation of approximately 1,822 m asl. Given its highly restricted known distribution and the absence of population data, the species should be provisionally classified as Data Deficient (DD) under IUCN Red List criteria. Targeted field surveys are urgently needed to evaluate its actual distribution, population size, and ecological requirements. Because green pit vipers are medically important, accurate taxonomic recognition of the *T. yunnanensis* complex is also critical for clinical identification and venom management.

In conclusion, *Trimeresurus loong* sp. nov. represents another lineage within the rapidly diversifying subgenus *Viridovipera* radiation of southwestern China. The discovery of this species, together with *T. nujiang* and *T. pretiosus*, highlights Yunnan and adjacent Himalayan regions as key centers of speciation for Asian green pit vipers. Integrative taxonomic approaches that combine morphological, molecular, and ecological data will be essential to fully resolve the complex evolutionary history of this medically significant group. This finding further reinforces the importance of southwestern China as a hotspot of pit viper diversification and highlights the need for continued integrative surveys in montane ecosystems.

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